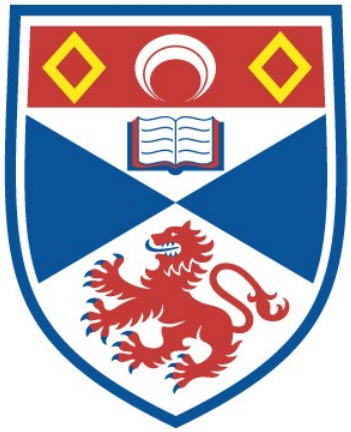
THE CONTEXT OF BEHAVIOURAL FLEXIBILITY IN CHIMPANZEES (PAN TROGLODYTES): IMPLICATIONS FOR THE EVOLUTION OF CUMULATIVE CULTURE

Sarah Jayne Davis

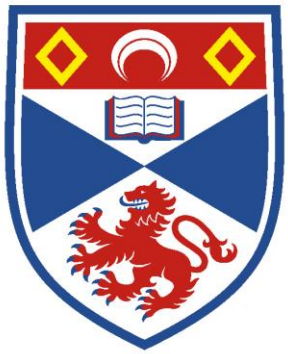
A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



2017

The Context of Behavioural Flexibility in Chimpanzees (*Pan troglodytes*): Implications for the Evolution of Cumulative Culture

Sarah Jayne Davis



University of
St Andrews

This thesis is submitted in fulfilment for the degree of PhD at the
University of St Andrews

June 2017

ABSTRACT

Cumulative culture is rare, if not altogether absent in non-human species. At the foundation of cumulative learning is the ability to flexibly modify, relinquish or build upon prior behaviours to make them more productive or efficient. Within the primate literature, a failure to optimize solutions in this way is often proposed to derive from low-fidelity copying of witnessed behaviours, sub-optimal social learning heuristics, or a lack of relevant socio-cognitive adaptations. However, humans can also be markedly inflexible in their behaviours, perseverating with, or becoming fixated on outdated or inappropriate responses. Humans show differential patterns of flexibility as a function of cognitive load, exhibiting difficulties with inhibiting sub-optimal behaviours when there are high demands on working memory. Here I present a series of studies on captive chimpanzees which show that not only is inhibitory control compromised in chimpanzees, but indicate ape behavioural conservatism may be underlain by similar constraints as in humans; chimpanzees show relatively little conservatism when behavioural optimization involves the inhibition of a well-established but simple solution, or the addition of a simple modification to a well-established but complex solution. In contrast, when behavioural optimization involves the inhibition of a well-established but complex solution, and especially when the alternative solution is also complex, chimpanzees show evidence of behavioural conservatism. I propose that conservatism is linked to behavioural complexity, potentially mediated by cognitive resource availability, and may be an important factor in the evolution of cumulative culture.

ACKNOWLEDGEMENTS

I would like to thank Andy Whiten for the endless support he has shown throughout my PhD. I'm extremely grateful to Andy for not only giving me the opportunity to pursue a PhD in a field I've been fascinated by for years, but for all the guidance and encouragement that he has given. I could not have asked for a better supervisor and can honestly say that Andy and his research are part of the reason I decided to come back to St Andrews and embark on this path.

I would like to thank all the care and research staff at the National Center for Chimpanzee Care, with a special thanks to Gillian Vale, who was an excellent mentor, a constant source of advice and encouragement, to Will Nyberg, who spent many hours repurposing and repairing apparatus, to Lisa Reamer, Susan Lambeth, Steven Schapiro, Mary-Catherine Mareno, Jenny Bridges, Mike Myers, Amanda Ott, Heather Webb and Erica Thiele. The dedication and love the NCCC staff have for the chimpanzees is truly reflected every day, and it was an absolute pleasure to work alongside both the staff, and of course, the chimpanzees. Many of whom became great friends.

I am grateful to Cristine Legare, who welcomed me into her lab when I was living in Austin, and who is not only a great person to work with, but a fantastic advisor. It was a pleasure to work with Cristine, Jennifer Clegg and Rachel-Watson Jones, with special thanks to Adam Alcott and Nicole Wen. I also thank Keith Haynes, Rob Mackinzie and Andy Burnley for their excellent craftsmanship in constructing chimp-proof apparatus.

I would like to thank my friends, especially Louise Campbell and Naomi McReynolds, who've been with me at St Andrews since 2008, and Sarah Pope, who first introduced me to the word Einstellung, and encouraged me to be more adventurous. Finally, I am so grateful to my family, and to my mother, who was always there for me. In fact, I only happened upon this PhD opportunity scrolling through the St Andrews Newsletter while bored in a waiting room as my mum underwent a root canal. Every cloud.

This thesis is dedicated to Kiht, Martha and Phoebe

1. Candidate's declarations:

I, Sarah Davis, hereby certify that this thesis, which is approximately 50,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September, 2013 and as a candidate for the degree of psychology in September, 2013; the higher study for which this is a record was carried out in the University of St Andrews between 2013 and 2017.

2. Supervisor's declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Psychology in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

3. Permission for publication:

In submitting this thesis to the University of St Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and the abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker, that my thesis will be electronically accessible for personal or research use unless exempt by award of an embargo as requested below, and that the library has the right to migrate my thesis into new electronic forms as required to ensure continued access to the thesis. I have obtained any third-party copyright permissions that may be required in order to allow such access and migration, or have requested the appropriate embargo below.

The following is an agreed request by candidate and supervisor regarding the publication of this thesis:

PRINTED COPY
a) No embargo on print copy

ELECTRONIC COPY
a) No embargo on electronic copy

ABSTRACT AND TITLE EMBARGOES

An embargo on the full text copy of your thesis in the electronic and printed formats will be granted automatically in the first instance. This embargo includes the abstract and title except that the title will be used in the graduation booklet.

If you have selected an embargo option indicate below if you wish to allow the thesis abstract and/or title to be published. If you do not complete the section below the title and abstract will remain embargoed along with the text of the thesis.

a) I agree to the title and abstract being published YES
b) I require an embargo on abstract NO
c) I require an embargo on title NO

Please note initial embargos can be requested for a maximum of five years. An embargo on a thesis submitted to the Faculty of Science or Medicine is rarely granted for more than two years in the first instance, without good justification. The Library will not lift an embargo before confirming with the student and supervisor that they do not intend to request a continuation. In the absence of an agreed response from both student and supervisor, the Head of School will be consulted. Please note that the total period of an embargo, including any continuation, is not expected to exceed ten years.
Where part of a thesis is to be embargoed, please specify the part and the reason.

CONTENTS

CHAPTER 4: A NOT B

CHAPTER 5: BIWAYS AND PITFALL

CHAPTER 1: GENERAL INTRODUCTION

1. CULTURE, CULTURAL TRANSMISSION AND CUMULATIVE CULTURE

The unparalleled achievements and evolutionary success of humans is widely attributed to our ability for cumulative culture: to take the discoveries, behaviours and technologies of others and further building on these, to create complex reserves of socially heritable knowledge and technology. Broadly speaking, culture may be termed as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland & Hoppitt, 2003, pg151). Without accumulation, culture will be limited to simple behaviours which are within the innovative capabilities of at least some individuals (Tomasello, Kruger & Ratner, 1993; Tennie, Call, & Tomasello, 2009; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). Such simple culture may confer survival or reproductive benefits over and above genetic endowment (Boyd & Richerson, 1985) but the ability to build upon, or ratchet up on (Tomasello et al., 1993), existing behaviours can often lead to substantial gains in productivity or efficiency (Boyd & Richerson, 1996). Whilst the ability to socially learn behaviours (defined as "learning that is influenced by observation of, or interaction with another animal (typically a conspecific) or its products" (Heyes, 1994, p. 207) may be common across taxa (Heyes & Galef, 1996; Hoppitt & Laland, 2013; Reader & Biro, 2010; Zentall & Galef, 1988) the ability to build on existing socially acquired behaviours is limited or absent in non-human animals. Seemingly, the most powerful form of this 'second inheritance system' (Whiten, 2005), cumulative culture, is uniquely highly developed in humans (Boyd & Richerson, 1996; Tomasello et al., 1993). This is most striking when we compare our culture to that of arguably the second most cultural species, our closest living relative, the chimpanzee (*Pan troglodytes*) (Whiten et al., 1999; Whiten, 2011).

The application of interdisciplinary research toward understanding the origins and evolution of culture in humans has proved powerful. Research focused on modern humans allows us to understand the processes through which we acquire cultural knowledge. Given how ubiquitous complex culture is within our species, the acquisition of culture in humans is most likely governed by phylogenetically endowed potential, that co-acts with a long developmental period to absorb, integrate and generate cultural practices, behaviours and technology. However, although we can learn much from studies of modern humans, to understand the origins of culture, research necessarily turns to comparative and evolutionary perspectives. This complementary research not only furthers understanding of the processes underlying acquisition of culture, but also when, why and how culture evolved.

A large corpus of work examining the origins of culture utilises both modelling and the experimental study of agents in simulated environments. In these two kinds of virtual worlds, the emergence, evolution and adaptiveness of behaviours are tracked, and the ensuing fitness of the agents assessed. Models thus act to reconstruct the environments that select for the correlates of culture, such as particular social learning mechanisms and strategies. However, modelling is, by necessity, over-simplified; to capture the processes underlying the evolution of one trait, noise within the environment must be drastically reduced to allow the systematic investigation of how specific environmental variables impact upon selection. In reality, agents are faced with an extremely complex environment, with many variables likely impacting upon their behaviours. It is therefore important that through the study of animals who share varying degrees of relatedness to us, we can examine the selection pressures and cognition that promote the emergence and maintenance of adaptive correlates of culture within complex and relatively ecologically valid environments. Much of my thesis will draw on comparative methodology to examine the cognition and cultural capacities of one of our two most closely related primate cousins, the chimpanzee. Given that we have shared much of our ancestral past with chimpanzees, comparison allows us to determine shared characteristics that may have been present in our common ancestors, and potentially phylogenetically endowed. It may also help delineate the origins of inter-species differences which impact profoundly on complex cognition and cultural capabilities.

1.1 ATTRIBUTING CULTURE

To say a species has culture, behaviours must not be attributable to genetic or ecological variables (Laland & Hoppitt, 2003). Somewhat akin to culture is the notion of a tradition. A tradition, as defined by Fragaszy and Perry (2003, p xiii) is 'a distinctive behaviour pattern shared by two or more individuals in a social unit which persists over time and that new practitioners acquire in part through socially aided learning'. Although there is some overlap between traditions and culture, some authors would be reluctant to label any species which shows the social learning of a single behavioural tradition as cultural. Instead, it is suggested that culture can be thought of as consisting of multiple and behaviourally diverse traditions (Whiten & van Schaik, 2007). Alternatively, it has been argued that only when social learning takes the form of human-like social transmission, notably imitation or teaching, may culture be attributed (Galef, 1992). Other forms of social learning may not provide high enough levels of fidelity to allow faithful transmission of cultural knowledge (Tennie et al., 2009, but see Caldwell & Millen, 2009; Franz

& Matthews, 2010). In sum, culture may be thought of as the existence of multiple and diverse traditions and which are socially transmitted with a sufficiently high level of fidelity.

1.2 WHY HAVE CULTURE?

The cognition underlying the propagation and maintenance of culture is expensive, involving a substantial investment of resources (Isler & Van Schaik, 2014). However, the ability to learn from others may reduce or circumvent the costs of innovation, and endow some species with a 'second inheritance system' (Boyd & Richerson, 1985; Whiten, 2005, pg 52). Although behaviours may be transmitted through genetic inheritance, this system may be informationally limited (Enquist & Ghirlanda, 2007) and, in many circumstances, slow to facilitate adaptation to relatively rapid changes in the local environment (Boyd & Richerson, 1985). Whilst in stable environments, genetically guided behaviour alone may suffice, the ability to both innovate and socially learn can afford an individual an adaptive advantage to adjust and survive in more variable environments (Boyd & Richerson, 1985, 1995, 1996). Culture has thus been proposed to underlie encephalization in the most intelligent animals, with expensive socio-cognitive mechanisms affording the perpetuation and acquisition of cultural knowledge (van Schaik & Burkart, 2011; Whiten & Erdal, 2012; Whiten & van Schaik, 2007; Whiten & van de Waal, 2017). However, dependence on cultural knowledge can also be non-adaptive or maladaptive (Rogers, 1988), whereby, for example, a suboptimal variant may spread through a population via social learning processes. To optimise utility in an information rich environment, we must implement mechanisms and heuristics which guide our behaviour and decisions (Boyd & Richerson, 1995; Enquist & Ghirlanda, 2007; Laland, 2004).

1.3 SOCIAL LEARNING MECHANISMS

Social learning may be accomplished through various mechanisms, each likely involving differing levels of socio-cognitive complexity. When attempting to define a specific social learning mechanism, there is a plethora of definitions to be found within the literature. This issue has been addressed in depth elsewhere (e.g. Whiten, Horner, Litchfield, & Marshall-Pescini, 2004), so I will briefly operationalise social learning mechanism based on previous discussions.

The transmission fidelity of cultural behaviours in a species may be very much dependant on the social learning mechanisms employed (Tomasello et al., 1993 but see Caldwell & Millen, 2009; Franz & Matthews, 2010). On one end of the social learning spectrum, where most non-human animals are expected to lie (Galef, 1992), learning from others is facilitated incidentally through local or stimulus *enhancement*; for example, individual B may leave a tool near a

foraging site which individual A then picks up and through personal exploration, learns how to forage successfully. Further along the spectrum lies emulation, where the learner observes and replicates *outcomes*; A does not copy the actions performed by B to achieve their goal, but only the end result of those actions. Although this social learning mechanism may result in the re-enactment of processes that the original practitioner (B in this case) was using to achieve the same outcome (Caldwell & Millen, 2009; Zwirner & Thornton, 2015) A will be effectively re-inventing (or reverse engineering) the process through personal exploration and trail-and error learning. However, when tasks are not constrained in the number of different ways an outcome can be realised, it is very likely that much variation will be seen in the processes utilised by individuals in a population (Caldwell, Schillinger, Evans, & Hopper, 2012; Derex, Godelle, & Raymond, 2012). This variation typically means that behaviours will be transmitted through a population with relatively low fidelity, which is considered a constraining factor on the spread, maintenance and advancement of complex culture (Enquist, Strimling, Eriksson, Laland, & Sjostrand, 2010; Galef, 1992; Lewis & Laland, 2012; van der Post, Franz, & Laland, 2017; Tomasello et al., 1993). Much information may be lost if the process underlying the outcome of interest is not replicated, and the behaviour is thus unlikely to be maintained in a population (Enquist 2012). In turn this affords less opportunity for the behaviour to be modified in a cumulative fashion (Lewis & Laland, 2012 but see Youn, Strumsky, Luis, Bettencourt & Lobo, 2015 who found use of a variant in modern humans was not correlated with how long that technology has been registered in the patent system); that is, modified to become more productive or efficient (Flynn, 2008). However, even if accumulation was to occur, this more productive or efficient innovation is unlikely to spread within the population due to a lack of process copying. As behaviours become increasingly more complex, they become difficult to re-invent and are practiced by only the innovator, disappearing from the population once the innovator emigrates or dies.

Approaching the other end of the spectrum, *Imitation* involves attending to and copying B's bodily movements or object manipulations (Whiten et al., 2004; see also Byrne & Russon, 1998), that is, attention is primarily focused on the *process* of achieving a result (Tomasello et al., 1993). This is a form of high fidelity copying: the imitator attempts to capture and replicate the technique used by practitioner, thus reducing variation of behaviour within the population, and allowing the acquisition of complex behavioural routines. Imitation is seen as the primary social learning mechanism underlying cumulative culture (Derex et al., 2012; Tennie et al., 2009; Tomasello et al., 1993; Wasielewski, 2014). However, imitation may have limits when behaviour becomes too complex: not only would an individual, with limited cognitive resources, find it

difficult to remember every witnessed component of an observed behaviour, but the learning environment may be too noisy to allow extraction of all the relevant information needed (Brass & Heyes, 2005; Nehaniv & Dautenhahn, 2002; Subiaul & Schilder, 2014). The observer may thus rely on either repeated learning attempts (Enquist et al., 2010; Whiten, 2015) incorporating both social and trial-and error learning (Boyd & Richerson, 1996; Galef, 2015; Henrich & McElreath, 2003; Whalen, Cownden, & Laland, 2015), and/or pedagogical cues from the practitioner, signalling the need to learn, and the salience of particular actions (Csibra & Gergely, 2011). This sensitivity to pedagogy, as opposed to an ability to imitate per se, has been suggested to account for the high levels of fidelity in the learning and practice of complex human behaviour (Castro & Toro, 2014; Csibra & Gergely, 2011; Morin, 2016), and is often synonymously used with 'teaching'. Caro & Hauser (1992) attribute teaching when i) individual B changes its behaviour in the presence of individual A; ii) B receives no benefit from their own behaviour; iii) A acquires relevant knowledge that it otherwise would not have acquired or acquires this knowledge at a faster rate than would otherwise be expected (a much broader view has been offered by Kline, 2014). However, teaching, while perhaps the most faithful and effective form of transmission (Morgan et al., 2015), reflects the sophisticated psychology of the teacher, whilst relying on potentially quite simple learning mechanisms within the learner (Thornton and Katherine McAuliffe, 2006; Franks & Richardson, 2006; Hoppitt et al., 2008).

1.4 SOCIAL LEARNING HEURISTICS

Although social learning capabilities are a vital prerequisite for culture, they are not sufficient to produce culture in itself. Indiscriminate social learning is unlikely to be adaptive in the long run and can lead to sub-optimal, if not maladaptive, behaviours (Boyd & Richerson, 1995; Enquist & Ghirlanda, 2007; Giraldeau, Valone, & Templeton, 2002; Mesoudi, 2011; Rogers, 1988). It is for this reason that social learning is most likely under the influence of certain biases (or strategies) such as from whom to copy and when to do so (Boyd & Richerson, 1995; Laland, 2004). Although there are a host of potential social learning biases that are employed across the animal kingdom (Rendell et al., 2011), I will here focus on those which have received much attention in developmental, comparative and model based investigations.

Mathematical models have shown that there exist a range of circumstances under which a bias towards copying the behaviour exhibited by the majority of the group will be adaptive (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Nakahashi, 2007; Nakahashi, Wakano, & Henrich, 2012 but see Eriksson, Enquist, & Ghirlanda, 2007). Copying the majority not only allows an individual to acquire information relatively safely but also serves to homogenise

behaviours within populations, creating community specific behavioural patterns (Boyd & Richerson, 1985). Whilst the former of these two functions suggests a learning strategy employed by naïve individuals to avoid the costs of individual learning, the latter function may emerge from a desire to conform, and thus serves some social function (Deutsch and Gerard, 1955).

Other biases that may be employed, although not mutually exclusive of majority biases, include copy-successful-individuals or copy-the-most-successful behaviour (Henrich & Boyd, 2001; Nakahashi et al., 2012). The former may be linked to prestige or dominance biases whereby the most prestigious or dominant individual is used as a model from whom others copy (Henrich & Gil-White, 2001; Laland, 2004). Intuitively, it would make sense to copy such individuals as their success may be an indicator of specialised knowledge (e.g. Mesoudi, 2008; Mesoudi & Brien, 2008); however, it is not always clear why an individual is successful and this could potentially lead to pitfalls (Laland, 2004; Mesoudi, 2011). Alternatively, one could employ the copy-the-most-successful-behaviour strategy which, although it avoids the incidental spread of sub-optimal behaviours and may be highly adaptive, would require the observer to evaluate behavioural pay-offs, a cognitively sophisticated capability (Laland, 2004; Nakahashi et al., 2012; Schlag, 1998).

As highlighted above, the types of learning biases employed may have a major impact on the cultural evolution of a species (Caldwell, 2015; Enquist & Ghirlanda, 2007; Laland, 2004; Marshall-Pescini & Whiten, 2008; Mesoudi, 2015; Schlag, 1998). For example, Mesoudi (2011) found that a strategy that biased learning towards copying the most successful behaviour led to the greatest levels of cultural complexity.

1.5 CUMULATIVE CULTURE

Without accumulation, culture will be limited to simple behaviours which are within the innovative capabilities of at least some individuals. Such simple culture may confer survival or reproductive benefits but the ability to build upon existing behaviours can often lead to increased gains or efficiency. As discussed in section 1.1.3, the ability to accumulate (or ratchet) on a socially transmitted behaviour over time is thought to be reliant upon highly faithful transmission processes (Derex et al., 2012; Lewis & Laland, 2012; Tomasello et al., 1993 but see Caldwell & Millen, 2009; van der Post et al., 2017). A behaviour building upon its predecessor would presumably be more complex in nature and only within the capabilities of a 'rare innovator' (Whiten et al., 2009). The resultant behaviour or artefact would be a multi-generational innovative process and not within the innovative capabilities of a single individual (Tennie et al.,

2009). It is because of this increasing complexity that imitation (and/or teaching) is necessary to allow other individuals to adopt the additional processes resulting in cumulative behaviours or artefacts. Cumulative culture is thus dependent on a multitude of factors: innovative capability, high fidelity social transmission, appropriate social learning mechanisms, and ultimately, the behavioural flexibility needed to relinquish, modify or build upon behaviour.

2. CULTURE IN HUMANS

As our ancestors moved out of their ancestral habitats, selection likely favoured the evolution of the psychology needed to occupy what has been dubbed the "socio-cognitive niche", and ultimately culminated in the hunter gatherer way of life (Tooby & Devore, 1987; Whiten, 1999a). The transition to hunting and gathering would have required not only selection for increased cognitive capabilities, but also the advancement of the social capabilities beyond that of our shared ancestors with extant great apes, likely inclusive of heightened group co-operation and tolerance, along with theory of mind advancement (Herrmann, Call, Hernández-lloreda, Hare, & Tomasello, 2007; Whiten & Erdal, 2012).

The trajectory of the socio-cognitive path our ancestors carved is evidenced by the artefacts they left behind (see Whiten, 2015 for a recent review). Historically, the manufacture of stone tools dates back to around 2.5 million years ago (Semaw et al., 2003), or potentially even further (de la Torre, 2011; Harmand et al., 2015; Lewis et al., 2016; McPherron et al., 2010). Although these Oldowan artefacts show stone knapping skill beyond that of other great apes there is little evidence of further accumulation in technology until the Acheulean phase some 1.6 million years ago (Stout, 2011). Although in relatively recent years our species has grown exponentially in population size and now exhibits a vast amount of cultural behaviours and artefacts, it must be considered that most of humans' evolutionary history took place before the advent of agriculture and settlements; it is the hunter-gatherer way of life that our genetic systems have primarily evolved to perpetuate and it is this endowment that we still likely capitalise on today.

From the first steps of hominids into the realm of cumulative culture, it is suggested that selection favoured cultural capabilities, resulting in an autocatalytic spiral of gene-culture co-evolution (Boyd & Richerson, 1985; Richerson & Boyd, 2005; Laland, Odling-Smee, & Myles, 2010; Morgan et al., 2015). These increased capacities afforded our ancestors the social-cognition necessary for creating and propagating more complex knowledge and technology, increasing the adaptiveness of culture, which would again act selectively on the genome. Whilst there is a large

literature on the extent to which genes and developmental processes affect the maturing phenotype, from a gene-culture perspective, it seems likely that modern humans, born amongst the most altricial of primates, inherit a unique potential to *learn* complex knowledge (Herrmann et al., 2007; Hopkins, Russell, & Schaeffer, 2014; van Schaik & Burkart, 2011; Karmiloff-Smith, 1998; Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014). Thus whilst many animals must rely on domain-specific cognition that emerges in relatively deterministic developmental processes, humans are born with the 'expectation' that they will be culturally inducted, acquiring extraordinarily complex knowledge and technology throughout development (although see Cosmides & Tooby, 2013).

The extent of such preparedness of the human mind for culture is unclear. Evidence from atypical developing populations suggests that emerging modularity in the adult brain is underlain by what may originally have been domain-general mechanisms (or building blocks), which were then co-opted by many brain functions (Baron-Cohen, 1998; Karmiloff-Smith 2009a, 2009b). This indicates that modularity emerges over development and is likely heavily influenced by the developmental environment. This is most vividly shown by cases of extreme neglect (such of that of Genie), where children show severe learning difficulties not easily explained through any genetic abnormality. Cross-cultural comparisons between developing children also hint at differences between the social-cognition of human populations, and warn on the pitfalls of ascribing culturally relevant behaviours as universal in humans (Berl & Hewlett, 2015; Clegg & Legare, 2016; Legare & Nielsen, 2015; Nielsen & Tomaselli, 2010). Whilst it may be that humans are born with some basic preparedness, it should be considered that from almost the moment humans are born, they are engaged by cultural agents who interact with them in ways atypical of any other species, marking the beginning of their enculturation. This makes it very difficult to disentangle the extent to which gene-culture co-evolution has prepared the brain to acquire culture through a propensity to employ certain social learning mechanisms and heuristics (Tomasello, 2016), or through the potential to allow the cultural environment to reliably influence the development of these skills (Barrett and Kurzban, 2006).

2.1 SOCIAL LEARNING MECHANISMS

Whilst humans are capable of many forms of social learning, and employ a portfolio of these mechanisms to socially acquire cultural behaviours (Whiten, 2017) it has been argued that high fidelity social learning mechanisms are at the heart of human culture (Galef, 1992; Tennie et al., 2009; Tomasello et al., 1993).

Imitation is apparent in human social learning from an early age, with preverbal infants showing imitative abilities (Gergely, Bekkering, & Király, 2002). With development, the degree of imitation exhibited by children (and adults) becomes even more pervasive such that is has been termed 'overimitation' (Horner & Whiten, 2005; McGuigan, Makinson, & Whiten, 2011; Nielsen & Tomaselli, 2010). When presented with novel tasks and shown how to solve these by adults, children are prone to copying not only relevant behaviours demonstrated but also functionally redundant ones as well, despite task transparency. In attempting to understand why children employ this apparently inefficient and ostensibly maladaptive learning strategy, it has been proposed that overimitation might be an extension of a typically adaptive learning process which allows the acquisition of complex culture without high cognitive demands (Kenward, Karlsson, & Persson, 2011; Lyons, Damrosch, Lin, Macris, & Keil, 2011; Lyons, Young, & Keil, 2007; McGuigan, Gladstone, & Cook, 2012; McGuigan et al., 2011).

Linked to high fidelity transmission, and children's impressive acquisition of knowledge and skills, is 'natural pedagogy' (Csibra & Gergely, 2011). These authors noted that children are very sensitive to cues which indicate an opportunity (or expectation) that they should attend to and learn the actions of another. This substantially reduces the noise in the learning environment, allowing more targeted learning. Notably, reports from modern hunter-gatherers suggest that transmission of skills relies heavily on observational learning, with the inference that natural pedagogy may guide the learning process (Hewlett, Fouts, Boyette, & Hewlett, 2011; Kline, 2014). However, in many countries, as children get older, they are in modern times provided with a 'formal education', where they are actively taught by members of the community. Given the opaque and increasingly complex cultural world we occupy, explicit teaching may be necessary to ensure that we acquire skills such as reading, writing and mathematics, inherent to modern Western culture.

2.2 SOCIAL LEARNING HEURISTICS

Social learning heuristics are the rules, biases and strategies used by the learning individual to guide when, and from whom to copy (Boyd and Richerson, 1985; Laland, 2004). Given the complexity and vastness of human cultural behaviour, we expect both modern humans, and our ancestors to have employed adaptive learning heuristics.

As previously discussed, the ability to recognise a more successful behaviour or individual is critical in cultural accumulation (Laland, 2004). A bias based on this ability would fit well with the progression of lithic technology: In a virtual simulation of the transmission of prehistoric

projectile points, Mesoudi & Brien (2008) found that the pattern of transmission suggested in Nevada's archaeological record was most likely generated from a copy-successful-individuals social learning bias. It was found that such a bias offered significant benefits over individual learning (Mesoudi & Brien, 2008) in environemnts were there were no costs to social learning, when participants flexibly switched between social and asocial learning, and where there existed several optimal projectile designs (Mesoudi, 2008). This is supported by Chudek, Heller, Birch and Henrich, (2012) who found children had a preference for more prestigious models (see also Wood, Kendal, & Flynn, 2012), as well as by Muthukrishna, Shulman, Vasilescu and Henrich (2014), who found that when multiple models existed in the population, individuals preferentially copied the most successful model's aretefact design. Interestingly though, participants here (Muthukrishna et al.) were observed to additionnally copy some aspects of other, less-successful models' behaviours, indicating that individuals may have been combining elements of multiple designs to generate their own novel ones (Derex et al., 2012; Enquist & Ghirlanda, 2007; Morgan, Rendell, Ehn, Hoppitt, & Laland, 2012).

Human social learning and decision-making appears to be heavily suscepetible to majority influences (Asch 1956), and interestingly Tomlin, Nedic, Prentice, Holmes and Cohen (2013) found that neural activity in the brain increased in areas typically associated with response uncertainty when human adults detected their behaviour differed from others. In line with models which predict the evolution of majority influences in virtual environments potentially reflective of those of our ancestors (e.g. Henrich & Boyd, 2001), experiments with children also suggest that we may have a culturally and/or genetically endowed tendency towards conformity (that is, adopting the views or behaviours of the majority despite contradictory personal information) (Haun and Tomasello (2011). That children are engaging in conformity as opposed to majority biased learning (that is, expressing responses based on perceived social expectations as opposed to responses based on true personal belief) is supported by Corriveau and Harris (2010), who found that children showed discrimination in the adoption of adult responses on a task depending on the consequences of their answers: no child adopted the incorrect adult response if the result was the drowning of a toy rabbit due to an inappropriately sized bridge. This is in line with Morgan, Rendell, Ehn, Hoppitt and Laland (2012), who found that conformity was also context dependent in adults.

Whilst this is by no means an exhaustive accout, humans, equipped with advanced socio-cognitive skills, appear to employ a multitude of social learning mechanisms and heuristics, and have the capacity to flexibly switch between these strategies (Derex, 2012; Laland, 2004; Morgan

et al., 2012; Whiten et al., 2004). It may be that this diverse repertoire, as opposed to reliance on any one social learning mechanism or rule, afforded our ancestors the capacity to maintain and build on their knowledge and technology.

2.3 CUMULATIVE CULTURE

The high fidelity social transmission processes of humans, along with the social learning strategies we employ, are thought to be responsible for allowing us to continually build upon the innovations of previous generations (Boyd & Richerson, 1996; Laland, 2004; Lewis & Laland, 2012; Mesoudi, 2011). When and how our ancestors acquired the ability to ratchet is still unclear. Although Oldowan technology exceeded the capabilities of extant wild great apes (cf Toth, Schick, Savage-Rumbaugh, Sevcik & Rumbaugh, 1993), it was not for another million years that we began to see significant advances in technology, with the advent of Acheulean technology. Yet still, it was not until around 160,000 to 40,000 years ago that we really see an explosion, at an unprecedented speed, in cumulative culture (e.g. Bar-Yosef, 2007; d'Errico & Stringer, 2011). It is likely that before this time, our ancestors, although perhaps capable of simple ratcheting, had reached some technological ceiling. What, then, changed?

Although there are several hypotheses, it has been suggested that the relatively advanced Oldowan technology overtook that of other species due to changes in hominin social organisation and demographics (Henrich, 2004; Muthukrishna, Shulman, Vasilescu, & Henrich, 2014; Pradhan, Tennie, & van Schaik, 2012; see also Hill, Wood, Baggio, Hurtado, & Boyd, 2014). Whether the changes in hominin cultural capabilities were driven by socio-cognitive advancements which led to changing demographics or vice-versa is hard to disentangle (Caldwell, 2015; Derex, Beugin, Godelle, & Raymond, 2013). Either way, the increasing sociality of hominins may have led to the advancement of already existent social learning skills such that, over time, stable and complex cumulative culture became possible, as evidenced by Acheulean and later technology (Pradhan, Tennie, & van Schaik, 2012; Whiten, 1999a; Whiten & van Schaik, 2007). This is consistent with models which suggest that cultural complexity is achieved when learners have access to large social networks of individuals (Enquist et al., 2010; Henrich, 2004; Powell, Shennan, & Thomas, 2009; Vaesen, 2012) and is supported by experiments examining the effect of the number of available models on skill advancement and cumulative achievements (Derex et al., 2013; Kempe & Mesoudi, 2014; Muthukrishna et al., 2014). With increasingly sophisticated social organisation, our ancestors would have been in a position to donate technology (such that a learner could forego steps within the ratchet) and allow for specialisation and division of labour within groups. Increased network size also means greater

opportunities to learn from innovators, via increasing the pool of innovators available (e.g. Henrich, 2004), as well as to share and collaborate on knowledge and technology (Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). Recent work suggests that partially connected networks, perhaps typical of our nomadic ancestors (Hill et al., 2014), increase the variation in problem solving strategies (Derex, Feron, Godelle, & Raymond, 2015). In tightly connected groups, once one idea is converged on, this idea may be perfected to a local optimum; however, this reduces the likelihood of continued exploration to find the best possible solution, or global optimum (Mason, Jones, & Goldstone, 2008; Selman, Kautz & Cohen, 1994). In loosely connected groups, there is less efficient transfer of information, such that groups are likely to converge on different local optimums. When these groups come together, through social transmission and collaboration, solutions may be moved closer towards the global optimum (Derex & Boyd, 2015; Lazer & Friedman, 2007 but see Mason & Watts, 2012), either through abandonment of sub-optimal solutions in favour of better ones, or through combining different components of each group's local solution (Boyd, Richerson, & Henrich, 2011). Indeed, multiple lines of evidence suggest that recombination of solutions from multiple models may be a key driving force behind cultural advancement (Derex et al., 2015; Youn et al., 2015). As such, demographic changes, increasing access to innovators, as well as increasing collaboration amongst different groups of hominids, could explain the explosion of cumulative culture seen in modern humans (Derex et al., 2013; Pradhan et al., 2012).

2.4 HUMAN CULTURE: CONCLUSION

Our ability to maintain, propagate and continually build on complex knowledge, skills, and technology has afforded our species with a highly advanced 'second inheritance system' (Whiten, 2005, pg 52). Our ability for cumulative culture has allowed us to far exceed the general intelligence of any other known species, to cultivate resources in an unprecedented way, and to modify our environment to fit our needs and convenience.

While this chapter has so far explored the basic facets of human culture, and speculated on how and why culture emerged in our ancestors, I have thus far commented little on the growing research that suggests social learning, and culture itself, are far from unique to humans (Whiten, 2017 for a recent review). While correlates of culture can be observed across a wide range of animals, the remainder of this thesis will focus on what we can learn from an animal with whom (along with the bonobo) we share our most recent animal ancestry: the chimpanzee.

3. CULTURE IN CHIMPANZEES

Attributing behaviours to culture in non-humans is often controversial. Some have argued that even if we accept that culture exists in other animals, these behaviours may be dependent on different governing processes and any similarities with human culture may be superficial (Galef, 1992). For example, it has been advocated that human culture is primarily transmitted through high fidelity social learning mechanisms, which may be dependent on uniquely complex cognitive capacities, such as theory of mind and an understanding of the goals of agents (Tomasello et al., 1993; Galef, 1992). Other species capable of social learning are typically thought to use lower fidelity social learning mechanisms such as emulation or enhancement, which constrain the spread and maintenance of cultural behaviours (Enquist et al., 2010; Lewis & Laland, 2012), making animal culture qualitatively different from our own. Further, even if a species is capable of high fidelity social transmission, humans may be unique in their reliance on certain social learning heuristics, such as copying the most successful behaviours or conspecifics, or being susceptible to majority influences.

It is perhaps by no coincidence that amongst the strongest of the candidate species to exhibit culture is one of our closest living relatives, the chimpanzee (Whiten et al., 1999). It may even be parsimoniously concluded that if chimpanzees display similar cultural correlates with us, or indeed any similarity with us in terms of cognition, developmental trajectories or brain functioning, that these may have been shared with, and potentially inherited in some form, from a common ancestor. The extent to which that form is genetically constrained in nature, or an inherited potential that with the right developmental environment, reliably emerges, remains to be seen. Importantly, comparative research with chimpanzees allows us to investigate the extent to which social and/or cognitive differences may have impacted upon our cultural capabilities, and specifically why humans may be unique in our capacity for cumulative culture; whilst evidence for culture in non-human species continues to grow, there are few candidate examples of cumulative culture outside of humans' distinctively complex achievements.

The first point I discuss here is whether chimpanzees possess culture. This depends in part on the definition of culture. Chimpanzees have the greatest number of known traditions outside of the human species, across foraging, tool use and social behaviours, with each chimpanzee group distinguished by their own particular cultural profile (Whiten et al., 1999). This would lead many, myself included, to consider chimpanzees as having culture. However, there is debate as to whether chimpanzees are capable of high-fidelity transmission, as well as the types of social learning heuristics they can employ. Although chimpanzees have been found to be capable of some degree of imitation (Buttelmann, Carpenter, Call, & Tomasello, 2007;

Horner & Whiten, 2005), these observations are often made of chimpanzees in captive conditions. This has led some to argue that when chimpanzees do display similarities with humans, it is most likely because they have been encultured by humans, and as such, their behaviour or cognition is not representative of a wild chimpanzee (Tomasello & Call, 2004). Additionally, although many accept that chimpanzees have group-specific behaviours, some have challenged whether these are underlain by culture, and argue that genetic or ecological underpinnings cannot be ruled out (Humle & Matsuzawa, 2002; Koops, McGrew, & Matsuzawa, 2013; Langergraber & Vigilant, 2011). Finally, unlike human culture, chimpanzees do not appear to possess significant cumulative culture. I will address each of these issues, and conclude that although there are differences between chimpanzee culture and our own, chimpanzees do possess culture, but their ability for cumulative culture is limited. I will discuss the multi-faceted reason as to why this is, before homing in on one major limiting factor: chimpanzees are behaviourally inflexible.

3.1 THE ENCULTURED CHIMPANZEE

I first address the legitimacy and validity of using chimpanzees in captive rearing environments to better understand both the chimpanzees mind and our own. A term often seen in the literature is 'encultured' chimpanzees (e.g. Buttelmann et al., 2007; Tennie, Call and Tomasello, 2012). It is suggested (most likely correctly) that captive, particularly human reared chimpanzees can have superior culture relevant abilities (such as imitative skill) owing to human interaction; that is, captive chimpanzees may undergo an enculturation process whereby humans affect their developing socio-cognitive skills (Tennie, Call, & Tomasello, 2012; Tomasello & Call, 2004). It is critical to note that the ontogenetic experiences of any animal that has an extended developmental period (such as chimpanzees and humans) are extremely important (e.g. Bjorklund, 2006). In fact, no animal has as long a developmental period as human children, and perhaps no animal's intelligence is as dependent or as sensitive to developmental processes as humans'. As discussed in section 2, from birth human infants are inducted into their cultures: We are encultured (Grusec & Hastings, 2007). We cannot take this for granted in comparative work, and assume that, as is often the case, abilities present in Western, Educated, Industrialized, Rich, Democratic ('WEIRD') children (Henrich, Heine, & Norenzayan, 2010) are phylogenetically endowed. In this vein, when attempting to identify inter-specific socio-cognitive differences between humans and chimpanzees, it is perhaps not fair to compare a wild chimpanzee to a child who has been raised in a highly pedagogical environment where socio-cognitive skills have likely been nurtured from birth. Perhaps more telling about chimpanzees'

shared socio-cognitive abilities are the studies which do focus on 'enculturated' chimpanzees, those who have been raised in environments as similar as possible to that of a human child. As Boesch (2007) highlights, interspecies comparisons should only be made when the participants have faced the same "ecological-imprint". Given that many developmental theories stress the importance of experience dependent organisation of the human brain, and ensuing cognitive functions (Baron-Cohen, 1998; Bishop, 1997; Karmiloff-Smith, 1998; 2009), it would seem unjust to call into question what studies on captive chimpanzee populations can really tell us about the origins of our own capabilities whilst selectively ignoring the effects of our own even more potent enculturation processes on children.

3.2 CAN WE RULE OUT ECOLOGICAL AND GENETIC EXPLANATIONS FOR REGIONAL DIFFERENCES IN BEHAVIOUR?

The attribution of culture is not only dependent on sufficiently advanced social learning mechanisms and strategies, but also through the ruling out of both ecological and genetic explanations of behaviour (Laland & Hoppitt, 2003; Laland & Janik, 2006; Langergraber et al., 2011). As van Schaik (2012) highlights, behaviours that are shared within communities but divergent between communities, may be due to independent but convergent genetic predispositions and/or behavioural plasticity in response to ecological cues. Whilst there are those who argue that genetic explanations cannot be ruled out when comparing chimpanzee populations (Langergraber & Vigilant, 2011; Langergraber et al., 2011), there is evidence to suggest that genetic explanations do not seem to be able to explain divergent behaviours between populations (Gruber et al., 2011; Luncz & Boesch, 2014; Luncz, Mundry, & Boesch, 2012). However the ruling out of subtle ecological causes of behaviour is perhaps more difficult (Humle & Matsuzawa, 2002; van Schaik, 2012a). That being said, there is evidence to suggest that at least some behaviours are also not explicable in terms of ecological influences alone and that some behaviours may be shaped by both ecological and cultural processes (Humle, Snowdon, & Matsuzawa, 2009; Koops et al., 2013); for example, migrating chimpanzees will sometimes adopt the local nut-cracking technique of their new group, relinquishing their own variant despite availability of the appropriate tools (Luncz & Boesch, 2014; Luncz et al., 2012). Overall, it would appear that an account of behaviour that incorporates culture may have more explanatory power than a genetic or ecological one alone.

3.3 SOCIAL LEARNING MECHANISMS

How do chimpanzees acquire socially available information? It has been strongly argued that chimpanzees primarily rely on lower-forms of social transmission mechanisms, such as emulation and enhancement. If true, this could explain a great deal of the cultural divide between our two species. Whilst like humans, there is little argument that chimpanzees are capable of emulation (e.g. Tennie, Call, & Tomasello, 2010), there is more debate over investigations which suggest they can employ multiple mechanisms of learning, including imitation. For example, chimpanzees may rely on emulation on simple tasks (Hopper, Lambeth, Schapiro, & Whiten, 2008), but on harder tasks, which have solutions outside of the innovative capabilities of most chimpanzees, they may also focus on and use process information (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014; Hopper, Lambeth, Schapiro, & Whiten, 2015; Horner & Whiten, 2005; Horner, Whiten, Flynn, & de Waal, 2006; McGuigan & Whiten, 2009). Other studies have arrived at the opposite conclusion, that chimpanzees have somewhat limited or non-existent imitative capabilities (Buttelmann, Carpenter, Call, & Tomasello, 2013; Call, Carpenter, & Tomasello, 2005; Tennie, Call, & Tomasello, 2012). These studies, in the very least, show there are marked differences between chimpanzee and human reliance on process information, with children being far more prone to imitate than chimpanzees. Whether they show a lack of imitative ability in chimpanzees is open to interpretation and debate. Interestingly, Buttelmann Carpenter, Call and Tomasello (2007), following Gergely et al. (2002)), found results consistent with chimpanzees having the capacity to understand the intention of another: chimpanzees appeared to be able to distinguish between actions which were incidental to a physical constraint, versus those which appeared to be purposefully selected as a rational course of action to achieve a goal. When actions appeared purposeful, chimpanzees were significantly more likely to imitate (Buttelmann et al., 2007). Of note here is that the authors consistently highlight that these chimpanzees were 'encultured' and that in a similar study conducted with non-encultured chimpanzees, there was no evidence of this sort of 'rational imitation' (Buttelmann, Carpenter, Call, & Tomasello, 2008). It is suggested that whilst all chimpanzees may be capable of understanding the intentions of others (e.g. Marsh & Legerstee, 2016) only some (the encultured) possess suitable motivational levels to attend to human actions, and this is a result of extensive human interaction (Buttelmann et al., 2008). This fits well with the observation that studies which find imitation (e.g. Horner & Whiten, 2005) are typically conducted with captive or semi-wild chimpanzees, and that those raised predominantly by humans tend to have socio-cognitive capacities well beyond those raised by their conspecifics (Tomasello, Carpenter & Hobson, 2003). However, the argument that only captive chimpanzees are imitators is offset by anecdotal observations of imitation in the wild; for example, Hobaiter and Byrne (2010) observed several

chimpanzees imitating the somewhat redundant method of using a liana to scratch their backs (instead of their hands) after observing a paralysed adult male using this technique to overcome his handicap.

Imitation, although thought to be one of the primary modes of cultural transmission in humans, is not the only high fidelity transmission mechanism available to us: we also teach. The occurrence of teaching in chimpanzees is limited and controversial. It has been suggested that young apes are already well equipped with other forms of social learning that negate the need for teaching (Hoppitt et al., 2008; Whiten, 1999b). That being said, there have been some putative cases of rare teaching displays in the wild; for example, Boesch (1991) reports cases in which a mother demonstrates correct technique after having noticed her infant struggle with nut cracking (see also Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). Perhaps whilst not routine educators, some apes may have the socio-cognitive capabilities required for teaching (Whiten 1999b). Although such teaching may not fall strictly within Caro and Hauser's (1992) definition of teaching, Byrne and Rapaport (2011) have argued that it is this intentional, targeted teaching that is most insightful in understanding the evolution of teaching in humans.

Another consideration is that chimpanzees do not rely on social information as much as humans do (van Leeuwen, Call, & Haun, 2014 but see Clement, Koenig, & Harris, 2004; Ma & Ganea, 2010). For example, Horner and Whiten (2005) showed that while chimpanzees can copy actions, they chose not to do so when they could instead emulate. Children on the other hand, copied wholesale all relevant and ostensibly irrelevant actions. This may due to childrens heavy reliance on social information (cf Haun, Rekers, & Tomasello, 2014), with children potentially employing an adaptive learning rule, such as copy-all/refine later (Horner and Whiten, 2005). This reliance/over reliance on social information to guide actions may be linked to children's sensitivity to pedagody (discussed in section 2.1). Chimpanzees may not be as susceptible to cues signalling an opportunity to learn as children are (although see Buttelmann et al., 2007), and are thus faced with a far noisier learning environment. If this is the case, the ability to parse relevant actions from social information may be harder for chimpanzees, which may explain that even if they are capable of imitation, emulation may be a more reliable form of learning.

In summary, findings are in line with the conclusion that chimpanzees possess a portfolio of social learning mechanisms (Price et al., 2016; Whiten et al., 2009) the use of which may be governed by certain parameters such as complexity and transparency of task; however, there are clear differences between the use of these mechanisms in humans and chimpanzees, with

humans having a greater tendency to not only use social information (Haun et al., 2014; van Leeuwen et al., 2014), but to predominantly rely on high fidelity mechanisms, such as imitation.

3.4 SOCIAL LEARNING HEURISTICS

The strategies employed by chimpanzees with respect to when and from whom they learn may also reveal important inter-species differences. Given the importance of majority based learning in the maintenance of cultural behaviours (Henrich & Boyd, 1998), it may be of significance that chimpanzees do appear to exhibit conformity to what may be perceived of as group norms, both within captivity (Bonnie, Horner, Whiten, & de Waal, 2007; Hopper, Schapiro, Lambeth, & Brosnan, 2011; Whiten, Horner, & de Waal, 2005) and in the wild (Luncz & Boesch, 2014; Luncz et al., 2012). For example, migrant females have recently been observed to relinquish their established nut cracking technique in lieu of a variant used by their new group to (Luncz & Boesch, 2014). However, this view of the conforming chimpanzee is not unchallenged (Vale et al., 2017; van Leeuwen & Haun, 2013); for example, when looking at the behaviour of a 'minority' group of chimpanzees after being exposed to an alternative 'majority' behaviour, van Leeuwen, Cronin, Schütte, Call and Haun (2013) found no evidence of conformity on a token deposit task. Although this may appear at odds with prior findings, it is worth noting that the behaviour of the majority was essentially the same technique as that of the minority. The majority either deposited tokens in a spatially separate location, a dimension within foraging where we might expect some necessary variability in group living animals who compete for resources, or the majority used visually different types of tokens. The visual differences between tokens may have been quite arbitrary to chimpanzees, who may not initially sub-categorise different types of tokens. This task may also be considered to be quite simple in nature. As such, a lack of conformity may draw parallels with findings in humans which suggest conformity is more likely to be seen on difficult tasks (Morgan et al., 2012). Also of note is that in humans the strength of conformity is positively correlated with the degree of consensus amongst demonstrators (Morgan et al., 2012). As chimpanzees in the minority group were exposed not only to majority behaviours but also the token solutions of other minority group members, we might expect a weakened propensity to conform.

Although chimpanzees may share other social learning strategies with humans, such as a preference to copy behaviours exhibited by the majority of conspecifics (Haun, Rekers, & Tomasello, 2012), and a proclivity to copy high prestige individuals (Horner, Proctor, Bonnie, Whiten, & de Waal, 2010) or dominant individuals (Kendal et al., 2015 but see Watson 2016), there do appear to be important inter-species differences. For example Marshall-Pescini and

Whiten (2008) speculated that chimpanzees might employ a copy-when-dissatisfied social learning strategy (cf Laland, 2004; Schlag 1988), after finding chimpanzees did not build on their behaviours to achieve greater rewards when they had a simpler solution which produced some payoff. However, recent studies have found contrary evidence that chimpanzees will relinquish a working solution (i.e. one that reliably produces reward) to adopt an alternative, higher pay-off solution (Hopper, Kurtycz, Ross, & Bonnie, 2015; van Leeuwen & Call, 2016; van Leeuwen et al., 2013; Vale, Flynn, Hopper, Lambeth, Shapiro & Kendal, in prep). Another explanation for Marshall-Pescini and Whiten's findings is that chimpanzees are conservative learners; that is, when chimpanzees have mastered a sufficiently rewarding behaviour, they lack the behavioural flexibility to modify that solution. This would have far reaching consequences for the cumulative capabilities of chimpanzees.

3.5 DO CHIMPANZEES' POSSESS CULTURE?

In summary, chimpanzees exhibit the greatest number of traditions outside of the human species, across foraging, tool use and social behaviours, with each chimpanzee group distinguished by their own particular cultural profile (Bonnie, Horner, Whiten, & de Waal, 2007; Gruber, Muller, & Reynolds, 2011; Hashimoto, Isaji, Koops, & Furuichi, 2015; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Humle, Snowdon, & Matsuzawa, 2009; Koops, McGrew, & Matsuzawa, 2013; Luncz & Boesch, 2015; Luncz, Mundry, & Boesch, 2012; van Leeuwen, Cronin, & Haun, 2014; Whiten et al., 1999; Whiten et al., 2007; Whiten, Horner, & de Waal, 2005). The social learning processes observed in chimpanzees do appear to be sufficient to transmit behaviours not only within, but between communities and then to maintain them (Biro, Inoue-Nakamura, Tonooka, Yamakoshi, Sousa, & Matsuzawa, 2003; Bonnie, Horner, Whiten, & de Waal, 2007; Gruber et al., 2011; Whiten et al., 2007; Whiten et al., 2005; van Leeuwen 2014), with some evidence that chimpanzees may employ similar social learning mechanisms and heuristics which underlie human culture (Price et al., 2016; Whiten, 2017; Whiten et al., 2009). These considerations strengthen the suggestion that the pattern of regional behavioural variants in wild chimpanzees is best explained by culture (Whiten et al., 1999). However, chimpanzee culture is not only quantifiably far more limited than our own, but it relatively simple in nature, with little evidence of knowledge, skill or technological accumulation (Henrich, 2015; Tennie et al., 2009). That being said, it is plausible that some behaviour exhibited by wild chimpanzees is the result of a cumulative process. For example, Boesch (2003) argues that nut cracking with the use of an anvil and stabilising stones is an elaboration on an ancestral hammering method. Similarly, Sanz, Call and Morgan, (2009) argue that simple,

unmodified tools were the precursors of more complex tools with design features such as brush tips. Further, complex tool kits are also employed by wild chimpanzees involving the use of several, multi-functional tools in sequential order, indicative of some form of cumulative build up (Boesch, Head, & Robbins, 2009; Sanz, Schöning, & Morgan, 2010). However, there is a lack of direct evidence that modern chimpanzees' forebears used any less elaborate methods than those seen today and thus this argument remains speculative (Dean, Vale, Laland, Flynn, & Kendal, 2013). Further, experiments attempting to look directly at the cumulative capabilities of chimpanzees have also not found promising evidence of such abilities (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Marshall-Pescini & Whiten, 2008). What is then constraining the evolution of chimpanzee culture?

3.6 WHAT IS LIMITING CULTURAL EVOLUTION IN CHIMPANZEES?

Section 1.2.4 provides something of an ultimate explanation as to why humans have cumulative culture: the choice undertaken in our evolutionary past to leave the familiarity of our ancient habitats, introducing the need to adapt to varied and novel environments. Unlike our own nomadic hominin ancestors, chimpanzees (and likely their own distinct ancestors) live in relatively stable environments, perhaps mitigating against the pressures needed for the expensive cognitive machinery underlying complex cultural evolution (Boyd & Richerson, 1996; Henrich & McElreath, 2003). However given that the beginning of cumulative culture in hominins may not have been due to changes in socio-cognitive capabilities per se (e.g. Pradhan et al., 2012) it may be that simple cumulative abilities were already within the socio-cognitive capacities of an ancestor shared with chimpanzees (Whiten et al., 2009). The question as to why chimpanzees have no or limited cumulative culture may, in this sense, be better addressed from a proximate perspective.

Chimpanzees do possess some of the 'raw ingredients' for cumulative culture, such as innovative capability (Nishida, Matsusaka, & McGrew, 2009; Reader & Laland, 2001), defined as "the discovery of novel information, the creation of new behaviour patterns, or the performance of established behavioural patterns in a novel context" (Reader & Laland, 2001, pg 788; Arbilly & Laland, 2017 for a recent discussion); however, long term field studies of wild chimpanzees indicate that while innovation may be common, most behaviours fail to spread throughout the rest of the population (Nishida et al., 2009; Yamamoto, Yamakoshi, Humle, & Matsuzawa, 2008; but see Hobaiter et al., 2014). This may be linked to the understanding that although chimpanzees potentially possess relatively advanced social learning mechanisms (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014; Hopper et al., 2007; Horner, Whiten,

Flynn, & de Waal, 2006), and adaptive biases for using social information (Van Leeuwen et al., 2013), it is likely that they employ these under far more limited circumstances than humans, with less intrinsic motivation to engage in social learning on the whole (Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Haun, Rekers, & Tomasello, 2014; Herrmann, Call, Hernández-lloreda, Hare, & Tomasello, 2007; Horner & Whiten, 2005; can Leeuwen, Call, & Haun, 2014; Nishida et al., 2009; Tennie, Call, & Tomasello, 2012; Tomasello et al., 1993). As such, the persuasiveness of the argument that chimpanzee culture is constrained by how they use social information is a powerful one. However, it is unlikely to be the whole story.

I end this chapter by highlighting what may be an important consideration when examining the limitations of cultural evolution. Notwithstanding the constraining impact of other core-prerequisites on chimpanzee culture, with relatively limited social learning mechanisms and heuristics resulting in a lack of behavioural upgrading, cumulative culture ultimately requires the ability to change established behaviours in order to adopt more efficient or productive ones; that is, in order to upgrade solutions, an individual must possess the behavioural flexibility to relinquish, modify and build on prior solutions. Behavioural flexibility has been defined as "the continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution" (Lehner, Burkart, & Schaik, 2011, pg 447). Behavioural inflexibility (or conservatism) may therefore in and of itself limit the evolution of culture. For example, imagine an agent solves a problem using Solution A. However, there is a better, more optimal way to solve the same problem by using Solution B. Solution B may be a completely different solution, a variant of solution A, or may build upon solution A. Despite the availability of B, the agent continues to use A. We can form two principal hypotheses as to why this might be:

Hypothesis 1: behavioural optimisation (use of Solution B) is hindered by having knowledge of a prior solution (A) i.e. behavioural inflexibility limits cultural evolution

Hypothesis 2: behavioural optimisation (use of solution B) is hindered by some other factor that prevents learning of solution B, but not solution A i.e. another factor limits cultural evolution

Within primatology, Hypothesis 2 is often adopted to explain why chimpanzees do not have cumulative culture. For example, when chimpanzees failed to relinquish a low-payoff solution in favour or a better one, Marshall-Pescini and Whiten (2008) suggested that chimpanzees did not build on Solution A *because* they were employing a copy-when-dissatisfied

social learning strategy. Similarly Dean et al. (2012) concluded that a lack of accumulation in chimpanzees was *because* of limited or absent socio-cognitive adaptations. While these accounts do have explanatory power, they also tend to be used in what is essentially a mediated relationship with behavioural inflexibility (Dean et al., 2013), overlooking that conservatism can be a cause in and of itself of sub-optimal behaviour (Hypothesis 1).

In order to distinguish between these two hypotheses, there needs to be some baseline measure of what behaviours we would observe if an individual had no prior experience of Solution A. Say our experimental group is trained to use Solution A. In subsequent testing, the more optimal Solution B is open to innovation, or may be socially learnt, but the experimental group continue to use Solution A. Here, we can reasonably say this group has failed to optimise their behaviour. This could be explained by Hypothesis 1 or 2. However, if we have a control group, who are not initially trained on Solution A, but are exposed to the same testing conditions as our experimental group, then we can infer some effect of having a prior solution on behaviour (as this is the only manipulated variable). If our control group all converge on A, the control group and the experimental group will be indistinguishable from one another, and thus we cannot say there was an effect of having a prior Solution A. Instead, we must attribute behavioural conservatism as an outcome of another factor which is affecting the adoption of solution B, for example, lack of innovation or social learning abilities (Hypothesis 2 supported). However, if our control group all converge on B, then we can conclude that there was an effect of prior solution A (Hypothesis 1 supported).

Tasks or observations which measure chimpanzees' ability to accumulate through modification, relinquishment or building upon prior solutions are essentially behavioural optimisation paradigms, which tap into cognitive and decision-making processes. By considering accumulation within the framework of "behavioural optimisation" and "decision-making", there is huge potential for understanding why chimpanzees do not have cumulative culture by comparing them to another often conservative species: our own.

CHAPTER 2: BEHAVIOURAL FLEXIBILITY

Behavioural flexibility has been defined as "the continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution" (Lehner, Burkart, & Schaik, 2011, pg 447). In chapter 1 I proposed: -

Hypothesis 1: behavioural optimisation (use of Solution B) is hindered by having knowledge of a prior solution (A) i.e. behavioural inflexibility limits cultural evolution

Hypothesis 2: behavioural optimisation (use of solution B) is hindered by some other factor that prevents learning of Solution B, but not Solution A i.e. another factor limits cultural evolution

Given the clear adaptive advantage of behavioural flexibility in solution optimization, that is, convergence on the best available solution, it remains something of a mystery as to why any species would exhibit highly conservative tendencies. Strikingly though, inflexibility in action or thought is not at all unique to chimpanzees, and is well documented in various forms and in varied degrees in human children (e.g. Carr et al., 2015; Defeyter & German, 2003; Jordan & Morton, 2012; Kirkham, Cruess, & Diamond, 2003; Zelazo, Müller, Frye, & Marcovitch, 2003), as well as in human adults (e.g. Bilalić, McLeod, & Gobet, 2008a; Bilalić, McLeod & Gobet, 2008b; Chrysikou et al., 2013; Diamond, 2005; German & Barrett, 2005; Gopnik, Griffiths, & Lucas, 2015; Luchins, 1942; Pope, Meguerditchian, Hopkins, & Fagot, 2015; Wiley, 1998). More often though, within the human literature, it is referred to as perseveration, functional fixedness or mental set (aka Einstellung). Notably, more distantly related species have at times shown greater flexibility in their behaviour than both chimpanzees (e.g. Huebner & Fichtel, 2015; Lehner et al., 2011), and humans (e.g. Pope et al., 2015; Vlamings et al., 2009).

1. PERSEVERATION, FUNCTIONAL FIXEDNESS AND SET

While I know of no formal distinction between different types of behavioural flexibility, I propose that perseveration, as used in development literature, and behavioural conservatism, as discussed within the non-human primate (hereafter primate) literature, draw close parallels with one another: both are linked to the continued use of outdated responses despite knowledge of a more appropriate alternative. Typically, studies with humans involve explicit instructions about the benefits of altering a response (or costs of maintaining the old one), whereas primate research often employs use of visual demonstrations. Functional fixedness, or mental set (also

referred to as cognitive set or *Einstellung*), may be more closely linked with innovation and creative thinking, specifically getting 'stuck' on the common usage of a tool or behaviour pattern, blocking solutions which would otherwise be easily generated (Defeyter & German, 2003); however this blockage should be overcome once *knowledge* of an alternative becomes available. The key distinction I draw is thus that cases of conservatism/perseveration involve information that a prior solution (A) is suboptimal, and there exists a specific solution (B), which is optimal. I will expand on these different types of flexibility below, and how we might relate this research to primate behaviour and cumulative culture. I will conclude that much research within the human literature indicates that behavioural conservatism, or perseveration with Solution A despite B, may be underlain by at least two determinants: availability of cognitive resources and heuristics guiding decisions.

1.1 FUNCTIONAL FIXEDNESS AND SET

Functional fixedness refers to becoming stuck ('fixated') on one common use of an artefact or tool. This fixedness blocks the creative thinking needed to innovate a new way of using the artefact, which without prior knowledge of function, would be easily discovered (Knoblich, Ohlsson, & Raney, 2001). Defeyter and German (2003) noted that this emerged during development in children (around age six), and was linked to children's maturing ability to conceive of objects as having a design. Cross cultural evidence suggests this 'design stance' may reliably emerge in humans, with evidence of functional fixedness in 'technologically sparse' cultures (German & Barrett, 2005; Margolis, Laurence, & Barrett, 2008). While usually this reliance on function may be adaptive when solving problems for which the artefact is relevant (cf DiYanni & Kelemen, 2008), when faced with situations where novel uses of an artefact must be generated, it can become a hindrance.

Interestingly, functional fixedness may not be unique to humans: Hanus, Mendes, Tennie and Call (2011) found evidence for functional fixedness in chimpanzees. When first faced with the floating peanut task (Tennie, Call, & Tomasello, 2010), chimpanzees failed to solve the task despite the availability of water from their drinking source. Oddly though, when presented with the task again, but this time provisioned with a new water source (i.e. one not previously associated with another function, such as drinking), some chimpanzees were able to solve the task. The authors suggest that prior knowledge of function (i.e. "this is for drinking") blocked the creative thinking needed to solve the task, which otherwise would have been solvable. It should be noted that only five out of the 24 chimpanzees tested were able to solve this task even when the new waterer dispenser was available, indicating that regardless of fixedness, the

task itself may have been rather difficult. This finding of fixedness is somewhat mirrored in the wild, where Gruber, Muller, & Reynolds (2011) found chimpanzees unfamiliar with using sticks for 'dipping' were unable to innovate this foraging strategy to dip for honey. In contrast, chimpanzees who were already adept at dipping with stick tools solved the problem readily. It was argued that chimpanzees' cultural knowledge shaped their foraging behaviour. This could tentatively support the hypothesis that functional fixedness is phylogenetically endowed in some form from a common ancestor, who may have also used tools and benefitted from this adaptation in some way.

Functional fixedness draws parallels with another type of fixedness, often referred to as 'set' or less commonly, 'Einstellung'. Here, knowledge of a prior solution (not necessarily of a prior function of a tool or artefact), prevents the creative thinking required to generate alternative solutions. Luchins (1942) originally studied this using a water jug task, where participants (adult humans) had to use three different sized water jugs to obtain a specific quantity of water. Having been previously exposed to a complex strategy for solution, participants rigidly stuck to this, as opposed to adopting a relatively simple alternative solution. Although Luchins (1942) originally reported that extensive practice does not contribute to the inability to flexibly think of new solutions, Crooks and McNeil (2009) found evidence to the contrary, with a correlation between response practice and flexible responding. Similarly, prior knowledge has been found to stall or delay convergence on the best game solution in chess experts (Britton & Tesser, 1982; Wiley, 1998), who become stuck on a local optimum. This curtails exploration of the problem space (see also Selman, Kautz & Cohen, 1994 for related discussions in artificial intelligence). Novices on the other hand, are able to outperform experts when global optima are easily found.

1.2 PERSEVERATION

Perseveration is a term widely used within the developmental literature, often referring to young children who having learnt one method of solving a task (Solution A), are encouraged or instructed to use another method (Solution B), but yet persevere with their initial solution (A). This mirrors the general methodology used when investigating cumulative abilities in apes (e.g. Marshall-Pescini & Whiten, 2008), with the exception that primates are necessarily provided with information of the alternative solution through visual demonstrations.

Tasks commonly employed to study perseveration are the Wisconsin Card Sorting Task (WCST), the dimensional change card sort task (DCCS), and Go/No-go. In DCCS, children are first asked to sort cards using a rule such as "sort cards by colour" (Solution A), then later asked

to sort the cards along another dimensions, such as "sort cards by shape" (Solution B). When the participant fails to relinquish Solution A, and switch to using the appropriate Solution B, they are classed as perseverating. Importantly, this is not because perseverators cannot learn solution B. In fact, when asked what the new sorting rule is, perseverators can correctly identify it immediately before proceeding to sort cards incorrectly. This finding is robust when counterbalancing for solution presentation. This strongly suggests that Hypothesis 2 cannot account for perseveration with solution B in these instances; rather there appears to be an effect of having a prior solution to the task (Hypothesis 1). Most telling though is that perseveration is associated with age. Quite robustly, three year olds perseverate with their old solution A, but five year olds are typically successful in switching to using solution B (Carlson, 2005; Zelazo, 2006; Zelazo et al., 2003). This is mirrored in another task designed to measure perseveration: Go/No-go. Here, individuals learn to respond to stimuli presented on a screen (go trials). On a minority of trials, generally after a string of go trials, a stimulus is presented which indicates that a response should be withheld (no go). Again, children commit more perseverative errors on this task than adults do (e.g. Cragg & Nation, 2008). It is this developmental trajectory that strongly indicates that perseveration is underlain by limited cognitive resources in key executive functions (Diamond, 2013).

2. BEHAVIOURAL FLEXIBILITY AND EXECUTIVE FUNCTIONS

Executive functions are "a set of general-purpose control mechanisms, often linked to the prefrontal cortex of the brain, that regulate the dynamics of human cognition and action" (Miyake & Friedman, 2012, pg 2). Changing behaviour is a multi-faceted cognitive process dependent on these functions, requiring attention to appropriate extrinsic or intrinsic cues indicating a change is required, the inhibition of the now outdated or inappropriate response, and the ability to switch from the old to the new response, which must be held in working memory; that is, information held in mind (For a review see Bari & Robbins, 2013; Diamond, 2013). While there is some disagreement concerning both the nature and distinctiveness of executive functions, commonly identified components within the literature include inhibition, working memory and switching (definitions are from Diamond, 2013, pg137):

Inhibition: "involves being able to control one's attention, behaviour, thoughts, and/or emotions to override a strong internal predisposition or external lure, and instead do what's more appropriate or needed"

Working memory: "holding information in mind and mentally working with it (e.g., relating one thing to another, using information to solve a problem)"

Switching/shifting: "changing perspectives or approaches to a problem, flexibly adjusting to new demands, rules, or priorities (as in switching between tasks)"

Tasks such as the WCST and DCCS tap into several executive function components, making it somewhat difficult to disentangle which components are underlying perseveration (e.g. Nigg, 2000). Importantly however, from this executive function perspective of behavioural flexibility, we expect flexibility of response to be affected through two mechanisms: response prepotency, and working memory load; respectively, the extent to which behaviour has been practiced, and the complexity of the behaviour involved (Grandjean & Collette, 2011; Roberts, Hager, & Heron, 1994; Roberts & Pennington, 1996). Extensive practice with behaviour is thought to cause it to become a predominant or prepotent response, that is "reflexive actions, either innate or well established through a great deal of experience" (Miller, 2000), making it more difficult for this behaviour to be subsequently relinquished through inhibitory processes (e.g. Crooks & Mcneil, 2009). Research also highlights how increased taxation or load on working memory affects the ability to adopt solutions (Beilock & Decaro, 2007; See also Gathercole et al., 2008). Crucially, not only might these two factors affect behavioural flexibility, but they may share some neural and cognitive resources (Barber, Caffo, Pekar & Mostofsky, 2013; Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Chambers, Garavan, & Bellgrove, 2009 (for a review); Hester, Murphy, & Garavan, 2004; McNab et al., 2008; Mostofsky et al., 2003); for example, it has been found that working memory load (linked to complexity of task) is associated with differential effects on inhibition, with increased load on working memory associated with greater difficulties in successfully inhibiting behaviours or adopting alternatives (Berger, 2004, 2010; Boudreau, 2000; Chmielewski, Mückschel, Stock, & Beste, 2015; Conway, Cowan, & Bunting, 2001; Davidson, Amso, Anderson, & Diamond, 2006; Grandjean & Collette, 2011; Hester & Garavan, 2005; Roberts et al., 1994; Stahl & Pry, 2005; Stedron, Sahni, & Munakata, 2005; see also Kane & Engle, 2003; Marton, Kelmenson, & Pinkhasova, 2008; Redick, Calvo, Gay, & Engle, 2011). Taken together, these studies indicate that the more complex the behaviours involved, the greater the difficulty in relinquishing an established response and adopting another, especially if an existing response is highly prepotent (Houghton and Tipper, 1994; Munakata, 2001). Importantly, this research strongly suggests that behavioural flexibility is a function of cognitive resource availability: perseveration is underlain by limited

cognitive resources in key executive functions, with high demands on working memory likely detracting from the resources needed for inhibition.

This ties in with a long running debate about how separable some executive functions are (Collette et al., 2005; Herd et al., 2014; Miyake et al., 2000; Miyake & Friedman, 2012; Munakata et al., 2011), and whether inhibition reflects a separable component of executive function, or whether inhibitory failures are a result of limited working memory. This can be roughly summarised as whether inhibition involves the active *suppression* of irrelevant information (i.e. an inhibition mechanism) versus the *amplification* of relevant information in working memory (i.e. inhibition as an expression of working memory) (see Bari & Robbins, 2013; Best & Miller, 2010 for reviews). For example, Miyake and Friedman (2012) examined inhibition, working memory and switching on a series of nine tasks which are thought to tap into each of these. These authors found that variability in tasks was underlain by three components: 'Common EF', 'Updating-Specific', and 'Shifting-Specific'. Here, there is no specific component unique to inhibition. Note that while perseveration is most often associated with inhibition problems (either through poor suppression or amplification of information), the lack of creative problem solving inherent to set and fixedness is more closely linked to the shifting, or task-switching, component of executive functions (Diamond, 2013).

2.1 WHAT DO WE MEAN BY LIMITED COGNITIVE RESOURCES?

Allocation of resources, or top-down governing of executive functions, is generally referred to as cognitive control, which encompasses the processes and mechanisms underlying the assessment of the problem environment, the extraction, retrieval and inhibition of information, and ultimately the behaviour required to achieve goals (Botvinick & Cohen, 2014). Due to its unique patterns of connectivity with many key regions of the brain, the prefrontal cortex (PFC) is thought to have "the ideal infrastructure for synthesising the diverse range of information needed for complex behaviour" (Miller, 2000, pg 59) and is ultimately seen as being at the centre of cognitive control. Allocation of resources to executive functions comes increasingly under PFC guidance with age (Best & Miller, 2010; Braet et al., 2009; Thompson-schill, Ramscar, & Chrysikou, 2009), with PFC maturation linked to both increases in working memory capacity and inhibition (Diamond & Doar 1989). For example, Thomason-schill et al. (2009), found adolescents were poorer at maintaining large volumes of information in working memory than adults, and that this correlated with less neural activity in key regions associated with working memory. Similarly, Braet et al. (2009) found key neural differences between adults and adolescents on a response inhibition task, with adults showing not only less errors, but

comparatively greater activity in frontal regions (see also Bunge, Dudukovic, Thomason, Vaidya, & Gabrieli, 2002). Taken together, much of this research suggests that children have less cognitive control than older adults, with differential patterns of neural activity, especially in the PFC (Baird et al., 2002; Bell, Wolfe & Adkins, 2007).

Interestingly, increased cognitive control is likely associated with a reduced ability to generate novel ideas to problems. For example, Chrysikou et al. (2013) while asking adult participants to state aloud uncommon uses of artefacts, used inhibitory transcranial direct current stimulation over the PFC to disrupt neural activity. Those with diminished PFC activity (and thus cognitive control) were better at generating novel uses, displaying less functional fixedness than those with fully functional PFCs. This fits well with the developmental trajectory of functional fixedness (Defeyter & German, 2003) and set (Pope et al., 2015), with increasing cognitive control likely responsible for directing problem solving strategies through reliance on prior knowledge (see also Mölle, Marshall, Wolf, Fehm, & Born, 1999; Reverberi, Toraldo, D'agostini, & Skrap, 2005). This delayed maturation of cognitive control may be a highly adaptive strategy, allowing for flexible learning (Gopnik et al., 2015; Thompson-schill et al., 2009); for example statistical learning, that is extracting information from the environment or detecting patterns, although typically inefficient, may allow fluid thought and the flexible acquisition of extensive bodies of knowledge, such as is required for language (Romberg & Saffran, 2010). In line with this trade-off between increased cognitive control and flexible learning, Doll, Hutchison, & Frank (2011) found human adults were overly influenced by prior instructions about the reward contingencies of a task, and would have performed better had they evaluated the outcome of their solutions without these biases. Importantly, evidence suggested the PFC likely guided learning through a confirmation bias, such that decisions were not made by overriding accurate encoded information, but by the disproportionate encoding of information that accorded with their prior beliefs.

2.2 EXECUTIVE FUNCTION IN CHIMPANZEES

Executive functions have also been proposed to underlie performance in chimpanzees on behavioural change tasks. For example, Vlamings et al. (2009) highlight how problems in inhibiting a behaviour, as opposed to any lack of conceptual understanding, may be reflected in poor task performance (see also Call, 2001). Importantly, a similar effect of cognitive load on inhibition processes as seen in children may also be observed in chimpanzees. Specifically, Seed, Call, Emery, & Clayton (2009) found that chimpanzees performed worse on a trap task, where participants had to avoid moving (and losing) food over a trap, when they were required to use a

tool to manipulate the apparatus as opposed to their hands. Seed et al. concluded this was most likely due to the need to hold additional relationships in mind when navigating the task with a tool. This indicates that, like humans, cognitive load may affect problem solving ability in chimpanzees (cf Seed, Seddon, Greene, & Call, 2012).

Further supporting the differential effects of load on chimpanzee behaviour are studies which have found a correlation with flexibility and cognitive resource availability. For example, Manrique and Call (2015) tested how quickly chimpanzees could switch from pushing a handle in the opposite direction to that which they had been previously trained. The initial directional response was likely highly prepotent (trained to a criterion of 100 slides), but both A and B solutions were *simple*, with low demands on cognitive resources (Manrique et al., 2015). While all but three of the 23 chimpanzees were able to successfully switch direction, both older and younger chimpanzees were slower to do so than chimpanzees aged between 9-25 years. Importantly, the authors counterbalanced which side chimpanzees were initially trained on, which indicates that having a prior solution impacted on behavioural optimisation (Hypothesis 1). The authors highlight how inhibitory control, as in humans (e.g. Bélanger & Belleville, 2009), may be compromised for both older and younger chimpanzees.

Inhibition has been directly measured in chimpanzees using an A not B paradigm, where chimpanzees first learn to reach toward location A, before having to inhibit this response and instead reach toward location B. Although chimpanzees have been reported as having excellent inhibitory control, reaching ceiling levels of performance on A not B (Amici, Aureli, & Call, 2008; Barth & Call, 2006; MacLean et al., 2014), the paradigm used (A not B) may not have adequately established solution A as being a prepotent solution. I suggest this weakens what we can say about inhibitory control from these studies and I address this issue in depth in Chapter 4. Another aspect of inhibition may come under the rubric of 'Self-control'. Overall, chimpanzees do not always perform well on tasks measuring self-control through delayed gratification, where participants must inhibit reaching for a reward to accumulate greater rewards (Beran et al., 2014). However, whether this measures inhibitory control per se, as opposed to some other variable, such as motivation (Padmala & Pessoa, 2010) or intertemporal choice, is unclear (Beran, 2015).

3. BEHAVIOURAL FLEXIBILITY IN CHIMPANZEES

Not-withstanding these studies, despite chimpanzees being our closest living relative, human models of executive function and cognitive control are not typically applied to explain

suboptimal performance (that is, the continued use of a lower payoff, or less efficient behaviour despite the availability of a better solution) in the highly intelligent chimpanzee. For the remainder of this chapter, I will review the literature on behavioural flexibility in chimpanzees. Throughout, I will place each study in the context of Hypotheses 1 and 2, and will conclude that very little research has included adequate controls for distinguishing between these. I will suggest that the degree of behavioural flexibility in chimpanzees is related to the nature of the solutions under investigation, which provides indirect support for Hypothesis 1. By drawing on literature investigating decision-making and cognitive control in humans, I will argue that we can better understand the context of behavioural flexibility by considering the underlying proximate mechanisms governing solution choice.

As a small caveat, I would like to mention that I focus only on studies where Solution B involves a more efficient or productive outcome in terms of food reward than Solution A. A distinction perhaps needs to be drawn between these investigations, and those which focus on behavioural change when Solution A and B are equally optimal in (food) outcome, but may vary along another dimension, such as potential social payoffs. For example van Leeuwen, Cronin, Schütte, Call, & Haun (2013, study 1a and 1b) and Haun, Rekers, & Tomasello (2014), cite behavioural conservatism as a potential reason as to why chimpanzees stuck to Solution A despite conspecifics employing solution B; however, in these studies there was no incentive to change behaviours other than for social reasons. Whilst such work shows important comparative differences in the use of social information, whether we would say chimpanzees are acting conservatively may depend on how we define conservative behaviour. To me conservatism suggests some sub-optimality in solution choice, not necessarily sticking to one solution; after all, if an agent has found the optimum solution, it would be optimal to stick and suboptimal to change. Given this, in my thesis I define conservatism as "a reluctance to give up a well-grasped technique, even if a more efficient one is available and the individual knows it is available, and even after the mastered technique is made ineffective" (Hrubesch, Preuschoft, & van Schaik, 2009, pg 216). However, to others conservatism may show closer ties to a preference for a first learned solution; for example a criticism of Whiten, Horner and de Waal (2005; as well as Hopper, Schapiro, Lambeth, & Brosnan, 2011), who found that chimpanzees who discovered an equally optimum Solution B, reverted back to Solution A. This reversion was originally suggested to reflect conformity to a group norm (Solution A), but was later argued to potentially reflect a preference for a first learned technique (Solution A). How or why such a preference would exist is something of a puzzle. If an agent has abandoned solution A, and invested in

mastering Solution B, this agent has already demonstrated relatively low levels of behavioural conservatism, and arguably a relatively low level of attachment to A as a solution. More investigation would be needed to say why there is a natural preference for A if B has also been mastered, and should focus on ease of use, how many times and how long both A and B have been practiced, and if Solution A is being primed through social demonstrations that precede A.

3.1 BEHAVIOURAL INFLEXIBILITY

In one of the first experiments to look directly at chimpanzees' cumulative culture capabilities, Marshall-Pescini and Whiten (2008) found that young chimpanzees failed to cumulatively build upon the successful but simple techniques they initially learned through observation. Five chimpanzees between the ages of 3 and 8 years first witnessed (from a human demonstrator) then practiced a probing foraging technique (Figure 1). Following mastery of this solution (median of almost 90 dipping solutions used across 4 days of training), participants witnessed a more productive technique; however despite 180 demonstrations of this more productive solution, all but one chimpanzee displaying marked behavioural inflexibility, persevering with their established sub-optimal foraging technique over subsequent testing. Of note is that the one participant who did build on their behaviour had independently discovered the probing technique during a baseline control condition. Thus it appeared that although the more productive solution was within the innovative capabilities of at least some chimpanzees, having knowledge and/or experience of a suboptimal prior solution hindered behavioural optimisation. It was suggested that this inflexibility may be underlain by a copy-when-dissatisfied social learning heuristic (Laland, 2004; Schlag, 1998): as long as chimpanzees are gaining some payoff (and are thus not dissatisfied), they are unlikely to use social information despite potential gains in payoff (Marshall-Pescini & Whiten, 2008). In contrast, had chimpanzees been employing a copy-when-better strategy, they would have been able to successfully build on their solutions, as is likely necessary for cumulative culture (Laland, 2004; Mesoudi, 2011). This suggests that behavioural inflexibility is an outcome of a suboptimal social learning heuristic, and not it and of itself a limiting factor on cultural evolution. However, as chimpanzees were not exposed to the same conditions during baseline as they were during the testing period (i.e. exposed to social demonstrations of Solution B both with and without prior Solution A; see section 1.3.4), we cannot easily distinguish between Hypothesis 1 or 2.

As discussed in section 2.2, I also highlight here two important methodological considerations in Marshall-Pescini and Whiten's study: solution prepotency, and solution complexity. Regarding complexity, there is no unitary concept of what makes one behaviour

complex and another simple, but I propose two metrics for which we might reasonably assume complexity. The first concerns the learning of new behavioural processes; for example, individuals familiar with simple mechanics, such as levers, or sliding doors, do not need to relearn *how* to pull or slide when confronted with novel problems requiring these responses. They must only learn the particular affordances of the new problem and then apply known behaviours (Byrne & Russon, 1998). In contrast, solutions which require novel action elements must be learnt through some form of process learning. Therefore, I class simple behaviours as those which are already well within the capabilities of the participants, and easily discovered by novices. Second, we might assume behaviours which require holding in memory several relations (or sources of variation) between objects, such as solutions involving multiple, non-arbitrary steps (i.e. steps which are not incidental to the task, such as walking to the apparatus, but which are deliberate manipulations), are more complex than behaviours which require fewer steps, and place higher demands on cognitive resources (Halford, Wilson, & Phillips, 1998). I thus consider solutions which are not easily adopted by novices, and which require relatively long periods of learning before mastery, as relatively complex. While in reality solutions sit along a continuum of complexity, this dichotomy between simple and complex is a useful heuristic for facilitating a first attempt to look deeper into the underlying cognition of conservatism.

While there is no benchmark I know of to say with certainty a response is a prepotent one, given the extensive practice chimpanzees in Marshall-Pescini and Whiten had with the dipping solution (median of almost 90 trials), it seems reasonable to assume that here Solution A was a highly prepotent response. It may also be reasonable to assume that the both Solution A and B were relatively complex. The dipping solution (A) was only discovered by two individuals (from 11) in a baseline control, and the probing solution (B) found only by one of these same individuals. Additionally, to better reflect cumulative culture, Solution B was methodologically designed to be more complex than the first learned dipping technique, involving additive, non-arbitrary steps for success. Overall, these results show that chimpanzees perseverated with a *prepotent* and *complex* Solution A in lieu of adopting a more optimal, *complex* alternative Solution B (Table 1).

Hrubesch et al. (2009) likewise found evidence of behavioural inflexibility in chimpanzees on a tool based foraging task. Hrubesch et al. (2009) found that once chimpanzees had mastered one foraging technique (A), they failed to relinquish this solution in favour of a socially demonstrated more efficient alternative (B). In this instance, Solution B behaviour did not require building upon Solution A, but rather relinquishing it entirely, and was well within a

chimpanzee's behavioural repertoire. Here, 13 chimpanzees were presented with tools to rake food towards them from a tray attached to the outside of their enclosures; however, some participants quickly realised that shaking the tray allowed them to acquire the food much more efficiently. Although 10 individuals initially employed the 'raking' method, most participants used this 'rattle' method. Overall, there were six generalists, who flexibly switched between both methods; there were three rattle specialists, and four raking specialists. As the authors had intended this to be a tool based foraging task, to prevent rattling, the tray was subsequently chained, disabling use of the rattle method. Despite raking being well within the repertoires of chimpanzees, the three rattle specialists were unable to flexibly switch to an alternative method; thus, so extreme was the behavioural inflexibility observed that even when an old technique became completely redundant (i.e. produced no reward), three chimpanzees perseverated in their obsolete behaviours rather than adopt an alternative solution. Given that chimpanzees persevered with their redundant technique without reward, the behavioural conservatism seen here is not easily explained by a 'copy-if-dissatisfied' social learning rule. Additionally, as the alternative solutions were within the behavioural repertoire of chimpanzees, it is unlikely that chimpanzees failed to upgrade their behaviours due to any deficiency in their ability to learn this behaviour. It is worth noting however that those who were rattle experts (all adult males) may have been less inclined towards raking in the first place as most other participants (N = 10) demonstrated an affinity for raking by using it either exclusively or concurrently with rattling. Indeed, the acknowledgement that there were six subjects who switched between raking and rattling suggests some behavioural flexibility.

Overall, proficiency or mastery of one technique (rattling or raking) was found to negatively correlate with the use of the alternative technique. Thus the title of the paper "Skill mastery inhibits adoption of observed alternative solutions among chimpanzees". However, as the authors note, the skill mastery of rattling between generalists and specialists was not significantly different. Additionally the proclivity to only rattle may actually be a result of being an adult male chimpanzee. Given this, I would suggest the finding of most interest in this paper concerns the raking specialists: despite rattling being more efficient in the first phase of the experiment (i.e. before the tray was chained), three individuals chose to exclusively rake. These three individuals became experts in raking, exceeding the raking productivity of the generalists. Thus we might consider skill mastery to be linked to behavioural conservatism only for the raking specialists, who persevered with a suboptimal Solution A despite the availability of a more efficient Solution B. While there is no baseline condition in this group, given the behaviours of

other group members, and the ease of rattling (evidenced through ready innovation and lack of variation in proficiency between participants), evidence could potentially support a Hypothesis 1 interpretation of a failure to optimise behaviour: behavioural optimisation is hindered by having a prior solution. However, given that the rakers continued to accrue rewards, we also cannot rule out that they may have been following a copy-when-dissatisfied social learning strategy (cf Laland, 2004; Marshall-Pescini & Whiten, 2008).

Are these behaviours prepotent and complex? I would propose that we consider raking here to be a *prepotent* response, given both prior experience with this technique by these chimpanzees (as reported in Hrubesch et al.), as well as continued use over ten hours of testing (data were analysed at the end of testing, with no reports of when skill mastery was achieved). I would also suggest that the variation in success rates when using raking may indicate it was a reasonably *complex* method. This is supported by Seed et al. (2009), who found tool use placed a high demand on chimpanzees' cognitive resources likely caused by having to co-ordinate tool use with the requirements of the task. Notably, unlike Marshall-Pescini and Whiten (2008), the alternative Solution B (rattle) for these conservative rakers was relatively simple. In contrast, the generalists, who were not as proficient as rakers, showed little conservatism. Importantly the lack of proficiency in raking suggests generalists had not mastered the complex nature of raking. Finally, we cannot argue that raking was a prepotent response for generalists, by way of their being generalists. I summarise these results and implications in Table 1.

Price, Lambeth, Schapiro, & Whiten (2009) also found evidence of contextual flexibility: chimpanzees who acquired a *complex* foraging technique through personal innovation displayed a greater degree of behavioural conservatism than those who acquired the same technique through social learning. Specifically, captive chimpanzees who had watched video demonstrations of conspecifics constructing a raking tool perseverated (as measured by a combinatory score) with this combined tool as a means to access a reward (Solution A), despite the availability of a more efficient method (Solution B) in subsequent testing sessions. In contrast, those who had innovated Solution A were not seen to perseverate in testing. The authors conclude that social learning, but not independent innovation of a solution, may result in the persistent use of this solution even at the cost of efficiency. It should be noted however that Price et al. considered (in statistical analysis at least) individuals who had been exposed to enough information to allow emulative social learning to not have socially learnt the solution. Reassignment of this group to the rubric of social learning is unlikely to result in any significant differences in the behaviour of socially and asocially acquired solutions. The method of analyses

used by Price et al. also perhaps makes interpretation of these results difficult: individuals were assigned a combinatory score on a scale from 0-14, meaning that combinations (the measure of perseveration) were scored relatively, and not absolutely. Due to these considerations, I find it difficult to say whether chimpanzees displayed behavioural conservatism, and whether results can distinguish between Hypothesis 1 and 2.

In a follow up study to Price et al. (2009), Vale et al. (2016) found that although after three years individuals pooled from Price et al.'s subjects were still displaying some conservative behaviours on an opaque transfer task (as ranked on the same combinatory scale as the original Price et al. study), they switched to Solution B on an identical transparent transfer task. This suggests that having a causal understanding of a paradigm afforded flexible responding (Horner & Whiten, 2005). Relatedly, transparency may also reduce the need to hold in mind opaque associations (i.e. knowing that a particular action has an outcome, but not knowing *how* that action produces the outcome) needed to successfully complete the task, thus reducing task complexity. It may also allow for an assessment of the effectiveness of a behaviour, providing feedback which reinforces or extinguishes the solution (Völter & Call, 2012).

Another study which has suggested elements of conservatism is Bonnie et al. (2012). Here, captive chimpanzees were faced with an artificial termite mound, from which they could fish for food rewards in holes. Despite depleting a number a holes, chimpanzees continued to return to these locations and attempt to forage. While this does suggest some conservatism with continual use of a suboptimal Solution A despite redundancy, it might be reasonable to assume that returning to sites that previously yielded rewards may be quite adaptive (Ban, Boesch, & Janmaat, 2014). Chimpanzees were also able to flexibly switch between foraging locations, suggesting that they were perhaps not displaying high levels of conservatism. While Bonnie et al., cannot disambiguate the cause of potential conservatism here, they give a considered discussion spanning both Hypothesis 1 and 2 explanations for their results.

Lastly, findings of behavioural conservatism were somewhat mirrored by Dean, Kendal, Schapiro, Thierry, & Laland (2012) using an open diffusion paradigm (which looks at the spread of a behaviour seeded by one individual through a population of conspecifics and is thought to better simulate the spread of behaviours in a culturally relevant context (Whiten, Caldwell, & Mesoudi, 2016; Whiten & Flynn, 2010; Whiten & Mesoudi, 2008). It was found that whilst children would readily build upon their behaviours (although over 40% of children did not show evidence of accumulation on this task), chimpanzees would not upgrade to observed alternatives (Solution B) despite potential gains in productivity. The authors concluded that the ability to

build on behaviour was correlated with key socio-cognitive capacities, including prosociality, teaching, communication and observational learning. However we should consider that floor effects in both accumulation and some socio-cognitive measures in chimpanzees make this claim somewhat tenuous. Ultimately, whether this finding is driven by inter-species variation, or solely the intra-species variation within children is unclear. Here, again we see that behavioural inflexibility is suggested to be an outcome of what is considered to be the actual limiting factor on cultural evolution (these socio-cognitive adaptations), supporting Hypothesis 2. Dean et al. concluded that behavioural conservatism could not explain the lack of accumulation seen here as chimpanzees continued to manipulate and explore the puzzlebox (unsuccessfully) after reward extraction. While Dean et al. did not provide appropriate baseline conditions to disambiguate Hypothesis 1 or 2, I would be inclined to agree that conservatism here may be an outcome of another limiting factor: namely, the suitability of this puzzlebox.

Dean et al. (2012) looked at chimpanzees' ratcheting potential using a paradigm, which although it had a *simple* initial Solution A (which was practiced over 30 hours before social information regarding Solution B was made available, thus likely resulting in high *prepotency*), the alternative, cumulative Solution B involved rather *complex* elements, such as dial turning and sequential actions requiring coordinated manipulations with both hands. These behaviours may be relatively simple to a child, who through their already extensive enculturation at 3-5 years of age have likely gained much experience with such mechanisms as dials and buttons; however, to a chimpanzee, some elements may have been outside of most individual's repertoires, requiring extensive training to master as a stand-alone behaviour, let alone a behaviour that must be combined in a causally opaque fashion with other elements in a complex sequence. Thus, I would conclude that it is likely chimpanzees displayed inflexibility because they could not learn the alternative solutions (Hypothesis 2), but without appropriate baselines, this remains speculative.

Whilst there is certainly a place for complex and opaque behaviours in the comparative study of human culture (Tennie, Call, & Tomasello, 2009; Tennie et al., 2012), by using tasks which require species atypical behaviours, such as dial turning, we may be underestimating chimpanzee potential for *simple* cumulative culture, the starting point for true cultural evolution (Enquist, Ghirlanda, & Eriksson, 2011; Pradhan, Tennie, & van Schaik, 2012). However, using behaviours that can be easily mastered by most individuals may hinder the extent to which we can extrapolate to cultural accumulation, given that cumulative culture is the building upon of socially acquired cultural variants that are presumably outwith the innovative capabilities of most

individuals (Tennie et al., 2009; Whiten et al., 2009). Interestingly though, it is these latter studies, those involving relatively simple solutions, which have produced the most evidence of behavioural flexibility in chimpanzees.

3.2 BEHAVIOURAL FLEXIBILITY

When solutions involve simple behaviours, chimpanzees have been found to modify their behaviours to improve productivity and efficiency. For example, Hopper, Kurtycz, Ross, & Bonnie (2015), Van Leeuwen et al. (2013) and Vale, Flynn, Hopper, Lambeth, Schapiro, Kendal (in prep) found that chimpanzees in token deposit and token exchange tasks flexibly switched between solutions to maximise payoff. However, it is worth noting here that in these studies, the original solutions (A) and the new, more productive solutions (B) were conceptually very similar - both involved the same behaviours of Solution A, with the exception of changing the type of token exchanged or the location the token was exchanged. This may, in part, explain the discrepancy with some of the work reviewed (Section 2.3.1), where the original behaviours (A) differed conceptually from the alternative more productive behaviours (B). As Yamamoto, Humle and Tanaka (2013) and van Leeuwen et al. (2013) highlight, behaviours might be easier to modify when alternatives are similar in "perceptuo-motor or cognitive complexity" (Yamamoto et al., 2013, pg 3).

A closer look at the results of these studies may also raise some further considerations. Although van Leeuwen et al. found some modification of behaviour, this was only observed in three of the six chimpanzees studied; thus there is evidence here for both flexibility and inflexibility. In the Vale et al. study, while chimpanzees did eventually relinquish use of one token type to adopt another, in the critical test condition chimpanzees initially responded at random. This random responding makes it difficult to tell how well chimpanzees categorized tokens into different types, and further if they had formed an association between token type and differential payoffs. Further, Vale et al. did not find key significant differences between critical groups which would convincingly suggest that social information of an alternative solution with a higher payoff affected participant behaviour. In terms of disambiguating between Hypotheses 1 and 2, neither van Leeuwen et al., Hopper et al. nor Vale et al. provided adequate controls to do so, with no comparison within the same testing conditions of responses between those with and without prior training on Solution A. Further, while Hopper et al. did provide evidence for pay-off motivated behavioural change, van Leeuwen et al. did not run the necessary control groups to show that chimpanzees modified their behaviour to increase payoff. Instead, this was inferred from three

individuals who eventually started using Solution B during a condition which had differential payoffs. This change may have been underlain by a motivation to increase payoffs, or may have been due to prolonged exposure to the paradigm, which could have potentially seen similar response change regardless of payoff (cf van Leeuwen & Call, 2016). Indeed, Whiten et al. (2005) found chimpanzees modified their behaviours during long exposures, with little incentive to do so. Further, neither Hopper et al. nor van Leeuwen et al. showed a convincing effect of social information on behavioural change (nor did they claim such an effect).

In summary (Table 1), these token tasks all start with an initial *simple* Solution A, which is well-practiced and likely highly prepotent: for example, van Leeuwen et al. trained chimpanzees to a criterion of 30 uses of Solution A, and further gave them another 10 hours over which to use A in a group setting (Study 1b). The alternative Solution B is a variant of Solution A, and so is also *simple.* Taken together, these studies suggest chimpanzees are not entirely rigid in their behaviour, but results are quite mixed, hinting both at flexibility and conservatism. This may be due to possible confounding variables, such as assumed categorization of tokens into types, as well unclarified effects of social information and payoff.

Further evidence for behavioural flexibility regarding increasing efficiency in chimpanzees has been found by Yamamoto et al. (2013). Here, nine captive chimpanzees were provided with straws which could be used to access juice. Four participants independently innovated a straw sucking technique whilst five used the less efficient straw dipping technique. The dipping participants were then paired with one of the individuals who had innovated the sucking technique. Yamamoto et al. found that four of the five dipping (Solution A) subjects subsequently switched to the more efficient sucking technique (Solution B) demonstrated. The authors suggest that the dipping subjects may have been dissatisfied with the relatively miniscule reward they were procuring and therefore may have been using a copy-when-dissatisfied strategy (Laland, 2004). This strategy would not involve an individual having to make any appraisal of their own actions' efficiency against those of another (Laland, 2004) and is in line with the findings of Marshall-Pescini and Whiten (2008). However, it may be observed from data provided by Yamamoto et al. (Table 2, pg 3), that only two subjects reliably or consistently used Solution A prior to the social learning phase of the study. Although this adds support to the suggestion that subjects were dissatisfied with the returns of the dipping technique, it does somewhat detract from the degree of behavioural flexibility that may be inferred; that is, if the behaviour was not an established and reliable response to a problem, then an individual can be predicted to be less likely to show conservative tendencies. This suggests that the initial response was *not prepotent.*

As for the complexity of the behaviours, I would consider both to be *simple*: Dipping is a species-typical behaviour, and straw sucking was innovated by almost half of the participants in Yamamoto et al. (Table 1).

Perhaps some of the strongest evidence for chimpanzee flexibility comes from a study by Manrique, Völter and Call (2013). Here captive chimpanzees readily relinquished old foraging techniques (A) when they became inefficient, and innovated new ones (B). As there was no social information available to participants, and as they quickly discovered solutions to the changing problem, I would suggest that these behaviours be considered *simple*. I would also tentatively suggest the behaviours are not *prepotent*, at they were only practiced 10 times in each case, over a 10 minute period at most. Here, as there is little evidence of behavioural conservatism, there is no evidence either way to support Hypothesis 1 or 2 directly: there is no indication here that Solution A hindered optimisation, or that any other variable did so either (Table 1).

Many of the studies above were conducted in order to investigate behavioural flexibility; however, many other studies can also speak to chimpanzee flexibility. For example, Horner and Whiten (2005) found that chimpanzees who had learned to use an unnecessarily complex behaviour to solve a puzzlebox would cease to perform irrelevant actions when they realised these acts' redundancy. Considering that here, both the initial and alternative solutions involved multiple elements which were socially demonstrated (perhaps taught), and perhaps not easy for a novice to discover (although there is no baseline information to corroborate this), I tentatively class these as *complex* solutions. However, as chimpanzees performed the original behaviour only three times before they modified it, these behaviours are *not prepotent* (Table 1). This study also highlights that children display remarkable inflexibility in ways chimpanzees do not. For example, Horner and Whiten (2005) found young children continued to perseverate with irrelevant actions despite their obvious redundancy. Such instances of perseveration may be best explained via Hypothesis 2: behavioural optimisation is hindered by an alternative factor. In these cases, it is likely humans are 'overimitating', employing what may usually be quite an adaptive social learning heuristic, affording high fidelity transmission. Support for Hypothesis 2 in these instances further comes from Wood, Kendal and Flynn (2013), who show that children will modify their behaviour on a puzzlebox when they are provided with demonstrations of an alternative solution (B) to their own prior one (A); however, when they are originally shown Solution A (as opposed to personally discovering A), they tend to copy Solution B wholesale, including irrelevant actions. In contrast, those who personally learn A are less likely to copy irrelevant elements. This fits with the framework of natural pedagogy (Csibra & Gergely, 2011),

and how pedagogy can hinder exploration of the problem space (Bonawitz et al., 2011). I return to this idea of how inflexibility may at times be a result of an adaptive strategy within the Discussion section (Chapter 7).

3.3 SUMMARY

While Dean, Vale, Laland, Flynn and Kendal (2013) have highlighted that behavioural conservatism may be a mechanism hindering cumulative culture (Hypothesis 1) or an outcome of another factor limiting culture (Hypothesis 2), to my knowledge no systematic review has tackled the reasons underlying the inconsistencies in chimpanzee behavioural flexibility. Considering the research reviewed above, I conclude that few studies have provided adequate controls to afford discrimination between Hypotheses 1 and 2, with many (barring Hrubsech et al., 2009) offering a Hypothesis 2 explanation somewhat by default. I present evidence to suggest that these investigations use solutions which vary along two dimensions - solution prepotency and solution complexity - and that variation in these produces a pattern of flexibility and conservatism consistent with that of perseveration found in our own species. I suggest these dimensions are key to understanding the context of chimpanzee behavioural flexibility, and must be considered when we extrapolate findings to chimpanzees' cultural capabilities.

As cultural traditions are well-established and long held behaviours that require some investment, not only in their continual employment but in that they are also sufficiently complex to necessitate social learning to acquire, it is worth considering how these dimensions are reflected in investigations of culture. Behaviours which are not well-practiced may not capture the reliability and longevity of which many cultural behaviours are used (Lewis et al., 2016; Mercader et al., 2007). This is especially pertinent with research suggesting that longevity of cultural variants is key to accumulation (Enquist & Ghirlanda, 2007). Likewise, behaviours which vary along the spectrum of complexity may capture different components of cultural behaviour, but only those solutions which tap into the hard-learned techniques pertinent to complex skills reflect the nature of technological accumulation. In short, we must be careful in how we apply results from studies examining behavioural flexibility to chimpanzees' capacity for cumulative culture. So far, we have some evidence that chimpanzees can use payoff related social information to flexibly adjust highly-practiced behaviour in token exchange (Vale et al., in prep) and token deposit tasks (Hopper et al., 2015;Van Leeuwen et al., 2013). We also have evidence to suggest that chimpanzees can modify simple behaviours to adopt alternative simple behaviours when prior solutions are somewhat practiced (Manrique et al., 2013; Yamamoto et al., 2013). However, the simplicity of these behaviours limits the extent to which we can evaluate the

complexities of behavioural flexibility that are important in the context of cultural evolution. The capability to flexibly modify and adopt new variants of the same functional behaviour is vitally important as it allows flexible foraging strategies to cope with spatially and temporally varying environments, as well as the complex social dynamics of chimpanzee communities; for example, migrating individuals may benefit from adapting their behaviours to the foraging strategies of their new community rather than persisting in old, and possibly outdated, variants (Luncz & Boesch, 2014; Luncz et al., 2015 also see van de Waal, Borgeaud, & Whiten, 2013).

On the other hand, we have evidence that chimpanzees can be highly conservative when confronted with both relinquishing well-established, complex, technical foraging strategies (Hrubesch et al., 2009), or building upon them (Marshall-Pescini & Whiten, 2008). Further, simple prior solutions may be persevered with when the initial solution is prepotent, and the alternative solution is complex (Dean et al., 2012). These well-established, complex solutions may be the very behaviours which more closely reflect the intricacies of culturally transmitted skills and artefacts.

4. CONCLUSION

Cultural behaviours, especially with regard to multi-stepped foraging patterns, or use of technology, are not only complex solutions, often requiring extensive socially facilitated trial and error learning (Derex, Feron, Godelle, & Raymond, 2015; Rieucau & Giraldeau, 2011; Whalen, Cownden, & Laland, 2015), but are so well-established that they persist over generations. Drawing from findings within human research, these might be the very types of behaviour we would expect to be the most resistant to change. Given this, we should be cautious about extrapolating results to chimpanzee (or any animal) culture from studies which find flexibility but which focus on behaviour that may not mirror complex foraging patterns or technology, the candidate behaviours for meaningful accumulation. Specifically, we need to consider how the cognitive processes underlying behavioural flexibility may be responsible for divergent findings, and how conservatism, and potentially culture stagnation, may be a function of cognitive resource availability.

In this chapter I have shown that despite similarities in the pattern of contextual flexibility exhibited by chimpanzees and humans, explanations typically used to account for behavioural conservatism in humans have not been applied to chimpanzees. Specifically, much research in humans suggest suboptimal behaviours, marked by perseveration, are caused by having a prior solution in and of itself. Conversely, research in chimpanzees often suggests suboptimal

behaviours are caused by another, sometimes unmeasured, variable. In section 2.1 and 2.2 I have highlighted how explanations rooted in cognitive resource availability and cognitive control are typically employed to explain *how* having a prior solution hinders optimisation, with factors such as response prepotency and complexity being key causes of perseveration. In section 2.3 I have mapped out how well chimpanzee flexibility fits onto that framework, with results varying along the dimensions of both prepotency and complexity. I therefore contend that notwithstanding other limiting factors (Hypothesis 2), chimpanzee culture may be constrained in large part due to Hypothesis 1, in turn linked to cognitive resource availability:

Hypothesis 1: behavioural optimisation (use of Solution B) is hindered by having knowledge of an alternative Solution (A) i.e. behavioural inflexibility limits cultural evolution

In the remainder of this thesis, I will present empirical work that supports my contention. In Chapter 4, I will present evidence that contrary to prior work, inhibitory control is compromised in chimpanzees. In Chapter 5, I will present evidence which directly shows that like humans, chimpanzees show differential patterns of flexibility as a function of cognitive load, exhibiting difficulties with inhibiting sub-optimal behaviours when there are high demands on working memory. In Chapter 6, I will present evidence that chimpanzee exhibit yet higher levels of conservatism when behaviours closely match those of simple cumulative culture: optimization involves not only the partial inhibition of a complex solution, but also the addition of a complex element.

Table 1
Summary of research findings

Paper	Solution A		A blocked	Action on A	Solution B	Conservatism	Author Hypothesis
Manrique & Call (2015)	Prepotent	Simple	Partially	Abandon	Simple	Varied	_
Marshall-Pescini & Whiten (2008)	Prepotent	Complex	No	Build	Complex	High	2
Hrubesch et al. (2009)- Rakers	Prepotent	Somewhat complex	No	Abandon	Simple	High	1
Hrubesch et al. (2009)- Generalists	Not prepotent	varied	Yes	Abandon	varied	Low	1
Bonnie et al. (2012)	Not-prepotent	Simple	No	Abandon	Simple	low	1 & 2
Dean et al. (2012)	Prepotent	Simple	No	Build	Complex	High	2
Van Leeuwen et al. (2013)	Prepotent	Simple	No	Abandon	Simple	Low	_
Vale et al. (In prep)	Prepotent	Simple	No	Abandon	Simple	Low	_
Hopper et al. (2015)	Prepotent	Simple	No	Abandon	Simple	Low	_
Yamamoto et al. (2013)	Not prepotent	Simple	No	Abandon	Simple	Low	2
Manrique et al. (2013)	Not prepotent	Simple	Yes	Build	Simple	Low	_
Horner & Whiten (2005)	Not prepotent	Complex	No	Streamline	Complex	Low	2

Literature Review. Solution A: Original solution used with two levels, Solution A prepotency, and Solution A complexity; A blocked: describes if A was still a viable solution once B became an alternative solution, or if it is was blocked off during testing. Action on A: describes what action needed to be taken on A, either abandoning A, building on A, or omitting/streamlining elements of A. Solution B: Solution B complexity; Conservatism gives a basic description of how readily chimpanzees changed behaviours, with low levels of conservatism linked to high behavioural flexibility and high levels of conservatism linked with marked perseveration with Solution A. Author Hypothesis is which hypothesis authors interpret their results to lend support to

CHAPTER 3: INTRODUCTON TO EMPIRICAL METHODS

1. COMPARING CHILDREN AND CHIMPANZEES

One obvious methodological difficulty in comparing findings between species is that much research in children is based on relatively abstract problems, which often involve holding in mind arbitrary rules (sort by colour, shape etc.). Although such studies reduce experimental 'noise', allowing for cleaner measures of cognitive processes, they may not adequately predict real-world problem solving strategies. In contrast, primate researchers within the field of cultural evolution often employ goal-oriented, behavioural problems, incorporating layers of personal and social information in complex group settings. While the former attempts to control for the potentially confounding effects of, for example, motor control and normative biases, the latter attempts to maximise external validity (and is more tenable for researchers working with animals such as chimpanzees who cannot be separated from their groups, or trained on computer interfaces). I do not attempt to tease apart what these differences in methodology may mean for comparison between these two different literatures; rather, I have taken the core findings from developmental research, and examined how these may explain the pattern of flexibility in chimpanzees using methods typical of primate cultural research (bar Chapter 4, which uses a simple executive function task).

As an aside, to begin investigating how these differing methodologies may impact results, I am leading an ongoing, interdisciplinary project in collaboration with the University of Texas, Austin comparing adult chimpanzees and developing children on a behavioural optimization task involving a puzzlebox. Surprisingly, while preliminary results overall support a cognitive resource account of flexibility, solution choice on the first trial alone (total of seven trials are given to solve this task) shows younger children are often quicker to optimize their behaviours than older children. This is contrary to predictions generated by simpler tasks looking at flexible responding in developing children, and highlights the multi-faceted nature of decision-making in problems which better approximate real-world, goal-oriented behaviours. I report these preliminary results in Appendix 1.

2. SUBJECTS AND HOUSING

Chimpanzees were group housed at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas M.D. Anderson Cancer Center in Bastrop, Texas, U.S.A. Groups size ranged from 5-10 individuals and were trained and tested in both their outside enclosures (ranging in size from corrals at 4,300 square feet to PrimadomesTM

measuring approximately 34 feet in diameter and 25 feet high) and indoor dens (ranging in size from 6 feet deep by 15 feet wide to approximately 8 feet and 8 inches deep by 9 feet wide). Individuals were given the opportunity to voluntarily participate and separate from their group for further training and testing purposes in their inside enclosures for a period of no longer than 30 minutes. Participants were not food or water deprived during training or testing.

3. ANALYSES

In Chapters 4 and 5, data were analysed using Bayesian methods generated by the 'rethinking' package in R (McElreath, 2016). The data reported in Chapter 6 were analysed and published using frequentist methods. This difference was due to the order in which data were collected, with the data of Chapter 6 analysed and published before data collection for Chapters 4 and 5. While frequentist statistics remain the most commonly reported in psychology, there is a growing push to move to other forms of analyses, such as Bayesian.

Frequentist statistics use data from a sample, for example the mean and standard deviation, to generate a sampling error. Typically, this error is multiplied by some value based on a sampling distribution (e.g. a z or t distribution) to generate a 95% confidence interval. This 95% confidence interval represents the bounds between which, if one were to re-sample the population 100 times, in 95 of those cases, one would expect to find a parameter value (e.g. the mean) that has a confidence interval which overlaps with the true population mean. The 95% confidence interval is often erroneously thought of as being equivalent to meaning "the values between which we can be 95% sure the true value of the population parameter lies within". This is not possible to state within a frequentist analysis, but more closely reflects what is possible with Bayesian analysis (reported below - although Bayesian methods do not assume there is any one true population value, but rather a range of values with different plausibility). Frequentist analyses are long-run analyses, which infer statistical difference from the likely frequencies with which we expect values to appear if we were to repeat the sampling procedure, and can only address the confidence of an interval, not the confidence of any one particular value being the most likely parameter value. For example, when testing for an effect of a condition, say the effect of prior Solution A on behavioural optimisation (converging on Solution B), we can run a t-test on two groups (one with prior Solution A and a naïve group who do not have experience with Solution A) to determine if these groups are statistically distinct. If our samples (groups) are drawn from the same population (i.e. null hypothesis: there is no effect of prior Solution A on time taken to converge on Solution B), we expect these samples to generate overlapping confidence intervals (although statistical tests are needed to verify a lack of a significant difference, as these confidence

intervals may only marginally overlap). Based on the differences between the variability of values within each of our samples, we can calculate a t-statistic, and, based on the t-distribution and our desired level of confidence (typically set at 95%), find the probability of getting that statistic if our samples are drawn from the same population. On the premise of being 95% confident that any difference did not occur by chance, if we were to re-sample each group, and again calculate the t-statistic (which takes into consideration the differences between groups), then in more than 5% of the cases we would find a t-statistic that crosses the boundary with 0 i.e. some samples indicate no difference between groups, some samples indicate those with prior solution took longer to converge on solution B, and some samples indicate those without a prior solution took longer to converge on B. This would suggest that our samples are statistically indistinguishable and drawn from the same population, and that any differences between groups are due to chance. In contrast, if less than 5% of those cases cross the boundary of 0, then we would say there is a significant difference between groups, with only a small chance ($P < .05$) that if we were to resample the populations, we would not find this difference. It is also possible to then generate a confidence interval of the likely differences between these populations; however, again, this only allows us to generate an interval within which we can be 95% confident. It does not address how plausible specific parameter values within this interval are.

Bayesian methods take into account the relative plausibility of parameter values to create a posterior distribution, which maps out the likelihood of a range of values the parameter could be. From this posterior distribution, thousands of samples can be drawn to produce the most likely value of a parameter, as well as a credible interval. To confuse matters, this credible interval is also commonly referred to as a confidence interval, and throughout Chapters 4 & 5, I report a 95% confidence interval generated through Bayesian analyses. This is the interval between which 95% of plausible values lie. The average value (or maximum a priori) reported is the most probable of all these. I chose to report results with this 95% confidence interval as these are conventional terms which are familiar to frequentist statisticians, and may be easier to interpret. While it is commonly known that the 95% significance level is based on an arbitrary value, failing to report this in the publication process may be seen as problematic. There is no test of significance within Bayesian analyses; instead, there are a variety of ways to interpret data, and following the advice given by McElreath (2016), I report my analyses in great detail and with transparency. This allows others to make their own inferences about what the data show. Bayesian methods allow powerful resampling of the data to generate predictions which take into consideration all plausible values of the parameter and attempt to capture population level

behaviours. How much these predictions deviate from the sampled data is reported. Model comparison techniques are also used to construct and choose between different models of the data. This involves inputting different combinations of parameters and seeing how well each predicts the data in comparison to the others. In my main analyses I report the models which carry most of the Akaike weight (i.e. best predict the data). So, for example, a model which does not include an effect of prior solution may better describe the data than a model which does include this effect, carrying more of the Akaike weight. This would indicate that there is no effect of prior solution. Alternatively, predictions can be generated for each group, with an average time taken to converge on Solution B for each. A confidence/credible interval can be generated around these and plausible overlaps between group times can be calculated. From this, we can quantify not only the differences between groups, but the probability of those differences occurring; for example, it would be possible to calculate the probability with which those in the naïve group took ten minutes less to converge on Solution B than the group who had prior experience with Solution A. Again, while there is no significance test, doing this allows the reader to determine what the data actually show.

One key component of Bayesian methods is that the model needs to be defined using parameter 'priors'. These are values (typically for the mean and standard deviation) of a parameter that the model is instructed to start with. So, to use an example from McElreath (2016), if I wished to know if there was a difference between the heights of men and women, I would likely construct a model based on a normal distribution, and include two parameters that reflect men and women's heights

$$Height = a + b\ (Female)$$

Here, the 'a' parameter reflects the height of men, and 'b' the effect being female has on height. If these are credibly different, we would expect a model to show that including this *b* parameter improves the predictive power of the model, and would earn most of the Akaike weight. We would be able to say what the most likely value of this parameter is, and provide an interval which incorporates 95% of plausible values. However, this model assumes no known knowledge about the heights of men and women, where in reality, we do have some information that both men and women are typically over one metre tall, and typically below two metres. We can introduce this knowledge to the model in the form of 'priors', which act to nudge the model in the right direction. This is similar to the fitness landscapes often used in modelling work, where agents can get caught and stuck on local optimums, failing to execute the search pattern that would have allowed them to converge on the global optimum.

$$Height \sim dnorm(mu, sigma)$$

$$mu < -a + b * female$$

$$a \sim dnorm(150, 25)$$

$$b \sim dnorm(0, 10)$$

This model reads that height is normally distributed with an average of *mu*, and standard deviation of *sigma*. *Mu* is equal to *a* for men, and *a* + *b* for women. The next two lines define the priors for *a* and *b*. In this example, *a* is normally distributed with an average of 150 and a standard deviation of 25. This captures the information we already know about heights falling within one to two metres. Here *b* is normally distributed with an average of 0, and standard deviation of 10. This informs the model to start by assuming there is no average difference between the heights of men and women, and that women's heights may vary with a standard deviation of 10 from those of men. Providing prior information allows the model to begin its search for the most plausible values of the parameters. The model tests the plausibility of these parameter values against the sample, and then updates the prior information to reflect parameter values which better predict the data within the sample. The model continues to do this, sampling and updating until it converges on the range of parameter values which best describe the data (the posterior distribution). We can then sample from this posterior distribution to generate predictions, such as the probability that a woman is taller than a man, or what the probability is that a man is likely to be 10 centimetres taller than a women. When there is a lot of data for the model to sample from, the original defined priors are easily overwhelmed, and make little difference to the results. When there is less data, as with many of my own studies which often involve groups with fewer than ten individuals, priors need to be more tightly constrained to values that are reasonable assumptions about the data. These priors will have a stronger effect on results, which supports the need for greater transparency in analysis. Although this seems subjective, if we do not assume any knowledge, we are still inputting priors, but they are ill-informed and allow the model to spiral off in potentially suboptimal directions, producing spurious results. For example, if we had the heights of only five males and five females, and we assume no prior knowledge, we are instructing the model to start with the assumption that the average height of a male is zero. With such a small sample size, the model may potentially fail to reach a sensible result due to taking a 'wrong turn' in the landscape, with less data to pull it in the right direction. To ensure consistency, my priors are based on the average and standard deviation of the naive group for each analysis.

In order to provide a thorough analysis, which is accessible to those with different statistical backgrounds, Chapters 4 and 5 are accompanied by supplementary material in Appendices 2 and 3, which not only describe how I analysed the data through Bayesian methods as outlined above, but include a frequentist analysis for each of the core results reported in these chapters. In chapter 5, I also provide results generated through Bayesian estimation and online software (http://www.sumsar.net/best_online/) for a Bayesian version of the t-test developed by John Kruschke (2013). I have included this as, unlike the Bayesian analyses generated through the rethinking package, these are based on objective priors, and assume no prior knowledge about the data. All these analyses are in basic agreement, except in one instance in Chapter 5: Pitfall Study 2.1, where the results of Bayesian Estimation differed from those of my main Bayesian (and frequentist) analyses concerning an effect of social information on behavioural optimisation.

CHAPTER 4: A NOT B

BEHAVIOURAL FLEXIBILITY IN CHIMPANZEES (*PAN TROGLODYTES*): INHIBITORY CONTROL IS COMPROMISED FOR WELL-ESTABLISHED BEHAVIOURAL ROUTINES

Sarah J. Davis[1,2], Steven J. Schapiro[2], Susan P. Lambeth[2], Andrew Whiten[1]

ACKNOWLEDGEMENTS

I would like to thank the NCCC care staff for their invaluable expertise and assistance throughout this project and for the high standard of care and enrichment given to the chimpanzees, making this research possible. I am very grateful to William Nyberg for his technical and logistical support. This research was funded by the John Templeton Foundation (Grant ID: 40128, to K. Laland and A. Whiten). Support for the chimpanzee colony came from NIH U42 OD-011197.

COMPLIANCE WITH ETHICAL STANDARDS

Ethical approval was granted for this study by the UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

[1]Centre for Social learning and Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, St Andrews, KY16 9JP, Scotland

[2]National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, the University of Texas MD Anderson Cancer Center, Bastrop, TX 78602, USA

ABSTRACT

The flexible adjustment of response is key to optimal exploitation of a changing environment, and at the foundation of cumulative culture. The ability to inhibit, or cease use of, a suboptimal response is a vital component of behavioural change. Here, we tested 38 captive chimpanzees on an A not B task designed to measure inhibitory control. Participants first searched for a reward they had witnessed hidden under a cup in location A (A trials). On a later trial, this location then changed (B trial). To successfully retrieve the reward, the individual had to inhibit a previous search pattern (at location A) and flexibly switch to searching at an alternative location (location B). Unlike prior studies, which typically use three A trials, this study used a minimum of 20 A trials before the B trial. A 15 second delay between the observation of the switching of location of reward (from A to B), and the option to search for the reward on the critical B trial, was also included, to look for effects of memory on response. Results show that while there was no effect of delay on search choice, chimpanzees only performed at chance on the critical B trials, in contrast to near ceiling performance on A trials. This indicates that chimpanzees have limited inhibitory control when they need to cease using a highly-practiced, or prepotent, solution. This may offer a partial explanation as to why chimpanzees sometimes perseverate with sub-optimal solutions, often referred to as behavioural conservatism.

1. INTRODUCTION

Inhibitory control, the ability to suppress or override a known response, is a vital component of behavioural flexibility: the ability to flexibly relinquish, modify or build on known behaviours. It is perhaps not surprising that greater inhibitory control has been linked to greater intelligence, with chimpanzees displaying evidence of being amongst the smartest of non-human animals (MacLean et al., 2014). Chimpanzees are known to be both highly innovative (Reader & Laland, 2001) and adept social learners (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009), with a relatively expansive repertoire of cultural behaviours (Whiten et al., 1999). However, chimpanzees at times display conservative behaviour, showing a marked tendency to stick to known behaviours rather than adopt more productive or efficient alternatives (Davis et al. 2016; Dean et al. 2012; Hrubesch et al. 2009; Marshall-Pescini and Whiten 2008). This has been proposed to limit their foraging strategies and technology to simple, non-cumulative behaviours. Yet, somewhat puzzling, chimpanzees typically do not show perseverative, or conservative, responding on tasks thought to reflect inhibitory control, at times even outperforming children (Vlamings, Hare, & Call, 2009). Here we report an experiment that may help resolve this apparent contradiction.

1.1 INHIBITION IN CHIMPANZEES

One well-established test of inhibitory control is the A not B paradigm: participants have the opportunity to reach for a desirable object placed under a container in location B, after having previously reached for it several times in the spatially distinct location A. Despite witnessing the object being placed at B, infant humans under one year of age (Diamond, 1985), and many non-human species (MacLean et al., 2014), often erroneously search at the familiar A location, making a perseverative search error. Chimpanzees typically perform at ceiling level on this task, correctly inhibiting their prior search behaviour at A, and flexibly switching to searching at B (Amici et al., 2008; Barth and Call, 2006). Such findings indicate that chimpanzees have relatively strong inhibitory control. Chimpanzees were not seen to perseverate on the A not B task; as in older children, the task configuration thus appears not to challenge adult chimpanzees' inhibition abilities. This suggests elements of chimpanzee executive function exceeds that of a young human infant, but we suggest the relevance of such findings to chimpanzee behavioural flexibility should be treated with caution (see also Beran, 2015).

One reason for caution is that in these tasks, chimpanzees typically reach for the A cup only three times. Given the limited number of A reaches, it may be that the search behaviour at

A is not established well enough to have become a highly prepotent response (cf Marcovitch and Zelazo, 1999). As behavioural inflexibility is often found on tasks which focus on well-practiced solutions (Davis et al. 2016; Marshall-Pescini and Whiten, 2008), we cannot rule out that chimpanzees may perseverate with prior behaviours due to limited inhibitory control. Here we present findings on a modified A not B task, which show that if the initial A response is highly practiced, chimpanzees perform at chance on the B trial. This suggests chimpanzees' ability to inhibit highly prepotent responses has limits, with real implications for their everyday lives, such as potentials for cultural change.

1.2 A NOT B: WHAT CAUSES PERSEVERATION?

The perseverative search error shown by young children in Piaget's A not B paradigm was first thought to reflect a lack of object permanence (Piaget, 1954), and the infant's belief that their actions affected the location of the object. However, more recent work suggests that this erroneous reaching is more likely linked to underdeveloped executive function. To solve the A not B task, "Children must inhibit their learned response to search at Location A, children must shift from the task of searching at A to searching at B, and update their working memory of the hiding event from Location A to Location B." (Marcovitch & Zelazo, 2009, pg 2). In line with different task demands of the paradigm, the exact cause of the perseverative response on the A not B task has been attributed to various mechanisms.

Dominant theories hypothesize that the perseverative error may result from a lack of an inhibitory mechanism, such that there is no active suppression of the prepotent response, typically due to immature executive function (e.g. Bjorklund & Harnishfeger, 1990; Dempster, 1992). The error may alternatively be due to limited memory functions (Beran, Beran & Menzel, 2005; Morton & Munakata, 2002; Munakata, 2001; Pushina, Orekhova, & Stroganova, 2005). It is also possible that the error is due to a combination of both these executive functions: inhibition and working memory may work together to produce the perseverative error, with the need to hold the new representation in mind (B), while simultaneously inhibiting the old search location (A) (Diamond, 1988; Diamond et al., 1994; Espy et al., 1999). Yet other theories hypothesize that the motor demands of the task itself (reach to A or B) may cause the error (Berger, 2004; Berger, 2010; Boudreau and Bushnell, 2000; Clearfield et al., 2006; Thelen et al., 2001).

Interestingly, introducing a time delay between the hiding of the object at B and the search response results in a marked increase in the rates of perseveration in young children (Clearfield et al.. 2009; Diamond, 1985; Pushina et al., 2005; Watanabe et al., 2012). With a delay,

individuals have to represent and store in memory the location of the reward over a period of time, something which appears to challenge the limited working memory of infants under 10 months of age. This thus indicates that working memory plays a key role in the perseverative response. However, increasing the motor demands on search tasks, while controlling for memory demands, has also been shown to have a detrimental effect on correct search behaviours, with increasing task complexity causing perseveration (Berger, 2004; Berger. 2010; Boudreau and Bushnell 2000). This indicates that the increased demands of the task (whether memory or motor) might detract from the resources needed for successful inhibition (Grandjean and Collette, 2011; Roberts et al., 1994; Roberts & Pennington, 1996). As children develop, so too does their cognitive capacity, potentially allowing for appropriate responding.

2. PRESENT STUDY

This study was not designed to further elucidate the cause of the perseverative error per se, but rather to re-examine inhibitory control in chimpanzees on the A not B paradigm in the context of increased prepotency of the A response. To heighten prepotency, participants searched at the A location a minimum of 20 times before presentation of the critical B trial. To examine the effects of task demand on perseveration, we introduced a time delay between hiding a reward at B and the opportunity to search, and compared results on the same task without a time delay.

2.1 METHODS

Participants

Thirty-eight chimpanzees completed the A not B task (11 males, mean age 31.67 years, range 13.21 – 50.59; participant demographics in Appendix 2 Table 1). Chimpanzees were tested in their indoor dens. Individuals were given the opportunity to voluntarily participate and separate from their group for a period of no longer than 20 minutes. Participants were not food or water deprived during training or testing.

Apparatus

A clear plastic sheet was attached to a black crate to form a horizontal surface. Three green squares (10 x 10 centimetres) were painted onto the sheet in a row. This ensured uniform placement of the cups throughout testing (two red 'Solo' ® cups were used). The crate could be manoeuvred back and forth from the mesh. The A location was on the right of the apparatus (from the participant's viewpoint), and the B location on their left.

Procedure

As prior research in both children and dogs has indicated that the perseverative error could be attributed in large part to pedagogical cueing from the experimenter (Gergely et al., 2016; Topal et al., 2008), SJD positioned herself centrally behind the apparatus, occluded her eyes by wearing dark sunglasses throughout testing, and faced directly ahead, avoiding orientation towards either the A or B location,

A trials The apparatus was set up out of reach of the participants. The two cups (A and B) were initially set on their sides behind their respective A and B locations (marked by green squares). Participants watched SJD place one grape at the A location. The two cups were then placed simultaneously over their respective locations, hiding the contents (i.e. the grape as for A, and no reward as for B). The apparatus was pushed forward so that the participant could reach toward and/or touch the cups. If the participant chose correctly (searched at A), SJD pulled the apparatus back, removed the cup covering the grape, and awarded the grape to the participant. The cup covering the B location was also then removed. If the participant chose to incorrectly search at the B location, the B cup was removed first, followed immediately by the A cup (revealing the location of the grape). The participant was not given the grape in these trials. If a participant did not respond within 30 seconds, the apparatus was reset and the trial coded as a 'fail'. After 20 consecutive correct reaches toward the A cup, the critical probe or 'B' trial was administered. If a participant did not reach correctly on 20 consecutive A trials, they were given up to 10 additional A trials, with the secondary criterion for inclusion set at 20 successful trials out of 30.

B trial On the critical trial, the grape was initially placed under cup A as above; however, before the apparatus was pushed towards the participant, the grape was visibly removed from under cup A and repositioned under cup B.

Two versions of this task were administered: In condition 1, there was no delay between placing the grape under the B cup and the presentation of the apparatus to the chimpanzees to make their search choice. In condition 2, there was a 15 second delay between the observation of the switching of location of reward and the presentation of apparatus to the participant. These conditions were counterbalanced and presented at least three weeks apart to minimize any effects of prior experience with the task. The participant was awarded the grape only if they correctly searched at location B.

Analyses

Records of the training and testing phases were both narrated and visually recorded using a HC-920 Panasonic camcorder, with responses coded through later video analysis. Reaching choices (A or B) were coded through movements toward, or direct contact with A or B cups. An analysis of interrater reliability using Cohen's kappa found excellent agreement ($\kappa = 1$) between two coders' judgement of reaching response on 10% of the critical B trials. Data were analysed using Bayesian binomial regression models, using the Rethinking package in R (McElreath, 2016). Frequentist analyses are reported in Appendix 2. Throughout analyses, a 95% confidence (or credible) interval is reported (the interval between which 95% of plausible values lie). The average value reported is the most probable of all these. Predictions generated by modelling procedures are also reported. These predictions are based on the sample data and attempt to capture population level behaviours. How much these predictions deviate from the sampled data is reported in Appendix 2. Model comparison techniques were also used to construct and choose between different models of the data, through inputting different combinations of parameters, and discovering how well each model predicts the data in comparison to one another. We report here on the models which carry most Akaike weight (i.e. best predict the data); however, for transparency, details and effectiveness of different models are reported in Appendix 2.

2.2 RESULTS

Participant inclusion and training

Meeting criterion for inclusion, there were 13 chimpanzees in the No Delay condition followed by the Delay condition, 18 in the Delay condition followed by the No Delay condition, four in the No delay condition only, and three in the Delay condition only (due to participant drop out).

Behaviours during testing

For those participating in both the Delay and No Delay conditions, eight chimpanzees always chose correctly on the B trial; six never chose correctly on the B trial; five improved their performance (i.e. did better on the second presentation of the task); twelve declined in performance (i.e. did worse on their second presentation). For those participating in only the No Delay condition, one did not choose correctly. For those in only the Delay condition, two did not choose correctly.

Modelling responses

No effect of delay on response Binomial regression models indicate that there was no credible effect of condition (No Delay versus Delay), and no interaction between order (i.e. 1st or 2nd presentation of the task) and condition on the probability of a participant making an error on the B trial. Models which included these effects performed worse than models without (see Appendix 2 for details of models); however, there may have been an order effect, with participants more likely to make an error on the second presentation of the task (median of 0.21 more likely to make an error on the second B trial, 95% confidence interval of -0.02 to 0.44; Appendix 2 Fig. 2). Given a potential effect of order, analyses were run including this effect. Additional analyses run without this order effect are available in Appendix 2.

Performance on B trial Performance on the B trial was found to be at chance (Appendix 2 Fig. 1), with a 0.49 probability of committing a perseverative reaching error (mean; 95% confidence interval between 0.38 and 0.61). Considering the effect of order, it was found that performance on the second presentation was worse (i.e. a perseverative error was more likely) than that on the first (Table 1; Fig. 1; Appendix 2 Fig. 2).

Table 1
Model predictions for probability of error on A and B trials by presentation order

Trial Type	Median	2.5%	97.5%
1st Presentation A	0.06	0.04	0.08
1st Presentation B	0.41	0.24	0.59
2nd Presentation A	0.03	0.02	0.05
2nd Presentation B	0.58	0.39	0.77

The median is the predicted average probability of error on the A trials and B trial for 1st and 2nd task presentations of the paradigm. 2.5% and 97.5% represent the 95% confidence interval of the probability of committing an error

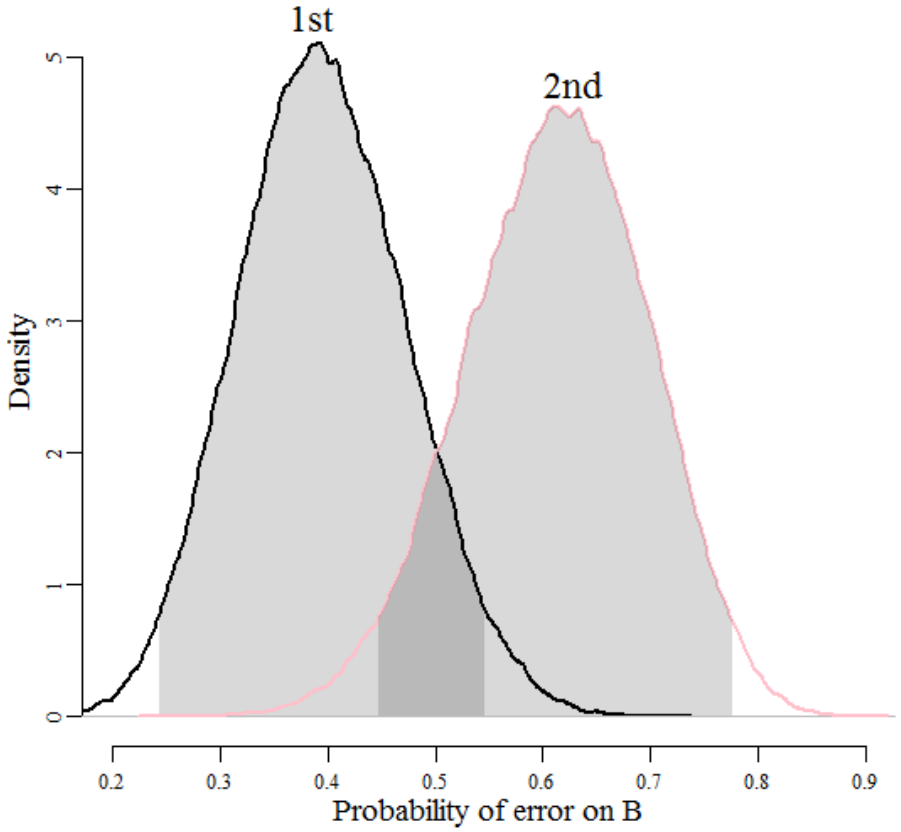


Fig. 1

Posterior distributions of probability of error on 1st and 2nd presentation of the B trial. Light grey shading shows the 95% highest posterior density interval for each trial; that is, the 95% confidence interval of the probability of committing an error. Dark grey shading shows the overlap in the marginal probabilities of error between presentations. The peaks indicate the most plausible probability of committing an error on the first task presentation (outlined in black) and the second (in pink)

Comparing performance on A trials and B trials It was found that chimpanzees performed credibly worse on the B trials (See Appendix 2 for further details), with a 0.45 median greater probability of making an error on a B trial than an A trial (95% credible interval of 0.31 – 0.59). Including an effect of order and an interaction effect between order and trial type (A or B trial) better predicted performance than including trial type (A or B) alone. Participants performed slightly better on the A trials during their second A not B task presentation (0.02 median reduction in probability of making an error, 95% interval of 0 – 0.05), but worse on their B trial (0.17 increase in probability of making an error, 95% interval of 0.07 – 0.41; Table 1; Fig.

2; Appendix 2 Fig. S5). This indicates that by the second presentation there was a greater tendency to reach for A, slightly reducing errors in A responses, but increasing the probability of an error on the B trial.

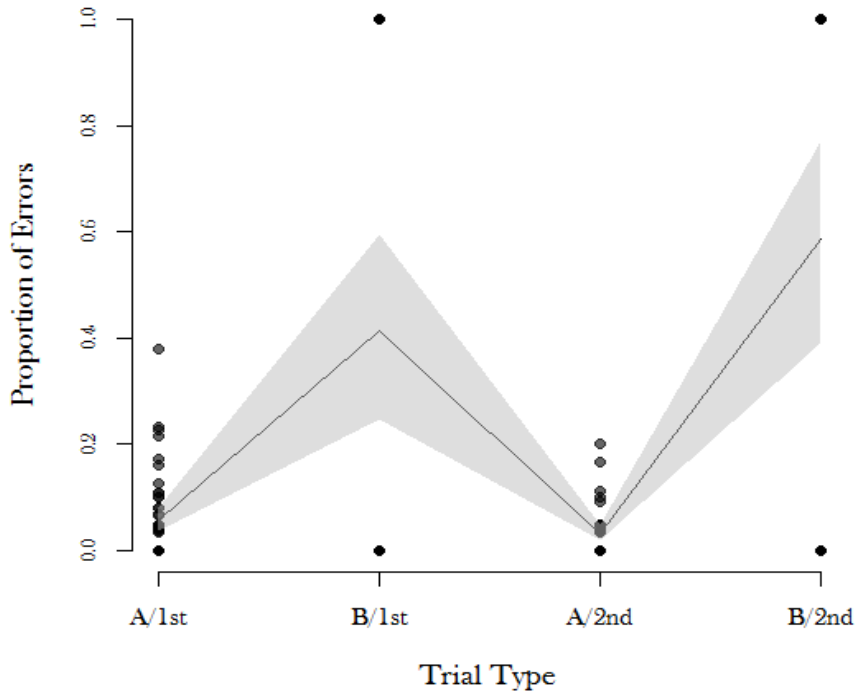


Fig. 2

Model predictions for trial type (A or B), order (1st or 2nd presentation) and an interaction between trial type and order. Black circles represent the observed proportion of errors made by participants. The black line is the mean expected proportion of reaching errors for trial type and order. The dark grey area is the 95% confidence interval of predicted proportion of errors

Performance on first A trial To investigate whether reaching on the B trial was a result of a lack of understanding of the contingencies of the task (participants may have learnt an associative rule such as "Reach to A location for a grape", instead of "Reach for grape"), we compared within task performance on the first A trial to the B trial. If chimpanzees did not understand that they needed to reach for the cup under which the grape was hidden, then we would expect performance to be at chance on the first trial. If instead, erroneous reaching on the

B trial is due to a perseverative search error, we would expect to see a credible difference between reaching errors on the first A trial and the first B trial.

The probability of making an error was credibly lower for the first A trial than it was for the B trial, with 0.33 greater probability of an error on the B trial (95% confidence interval of 0.18 to 0.48 greater probability of error on B than the first A trial; see Appendix 2 for further details). Including an interaction effect with order (which best predicted the data; see Appendix 2), we found similar results (Table 2; Fig. 3). Performance between the first presentation of the task and second presentation was not credibly different when we consider only the first A trials. We thus report on the first A trial collapsed across presentations one and two. While performance was credibly worse on both B trials than the first A trial, an interaction effect indicates performance was even poorer between the A trial and the second task presentation B trial (Table 2). Overall the difference between making an error on the first A trial versus the B trial was lower for the first task presentation (median 0.23 greater chance of making an error on B than A, 95% interval 0.06 – 0.41) than for the second presentation (median 0.45 greater chance of making an error on B than A, 95% interval 0.25 – 0.63).

Table 2
Model predictions for probability of error on 1st A and B trials by presentation order

Trial Type	Median	2.5%	97.5%
1st A (collapsed)	0.16	0.08	0.25
Presentation 1 B	0.39	0.24	0.54
Presentation 2 B	0.61	0.44	0.78

The median is the predicted average probability of error on the A trials and B trial for 1st and 2nd task presentations of the paradigm. 2.5% and 97.5% represent the 95% confidence interval of the probability of error

No effect of age While those who committed preservative errors were predicted to be older (median of 4.2 years), this difference was not found to be credible (95% confidence interval of -1.75 to 10.18 years; Appendix 2 Tables 10 and 11; Appendix 2 Fig. 9).

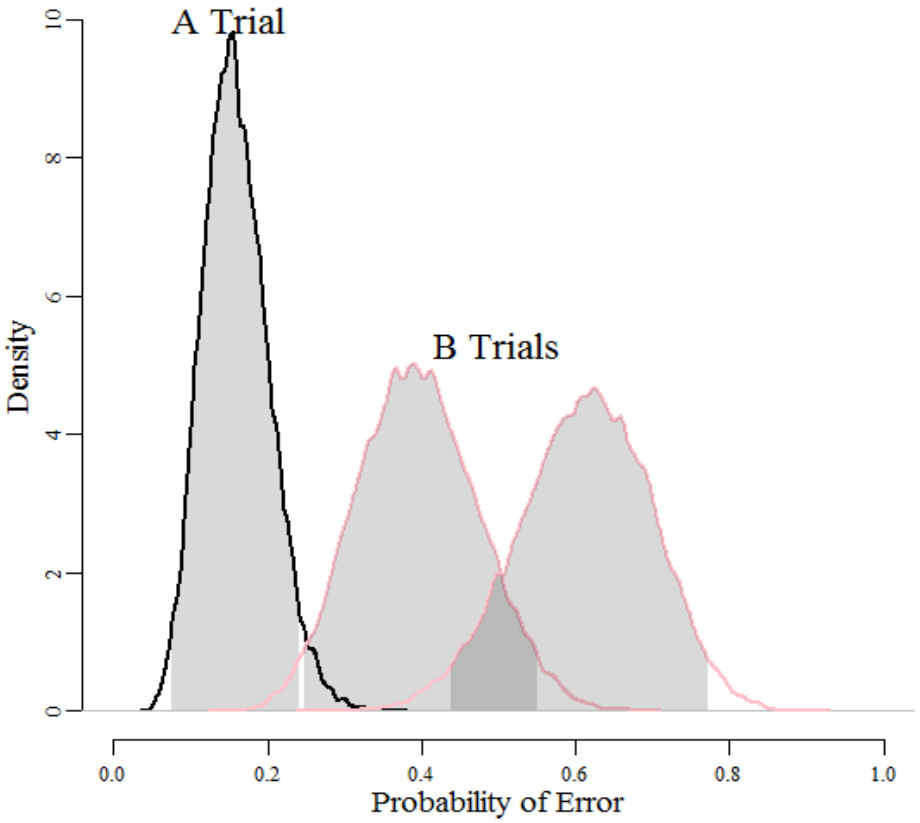


Fig. 3

Posterior distributions of probability of error for first A and B trials. Light grey shading shows the 95% highest posterior density interval for each trial. Dark grey shading shows the overlap in expected marginal probabilities of committing an error between trials. The black outline reflects performance on first A trials (collapsed across presentations) and pink for B trials on 1st and 2nd presentations

3. DISCUSSION

When chimpanzees had a well-established initial search pattern of reaching for A, they displayed difficulty inhibiting this response and flexibly switching to searching at the new B location. Chimpanzees performed near ceiling level on the A trials, but at chance on the B trial. Although delaying presentation between a hiding event and opportunity to search has been found to result in erroneous searching in chimpanzees (Barth & Call, 2006), we did not find an effect

of delaying presentation on the B trial. This is perhaps because chimpanzees here had only a 15 second delay, instead of the 30 seconds in the study of Barth and Call (2006). However in our own study, the high prepotency of the initial response alone was enough to reveal an inhibition issue without the additional taxation on working memory. Our finding no effect of delay on task performance suggests that the perseverative errors seen here were a result of an inhibition problem, as opposed to limited working memory per se.

That chimpanzees did not perform at chance on their first A trial indicates they understood the contingencies of the task, and did not need to learn how to solve the task via associative learning or some procedural rule. However, although there is little indication that chimpanzees did not understand the task, we should consider habit formation as one reason we see a perseverative error. Research suggests that whilst behaviours may begin as goal-oriented responses (such as 'reach to the location of the grape'), there may be a gradual crossover from this action-outcome responding (model based), to more habitual responding (model free). Smith and Graybiel (2016) highlight that while initially the brain prefers to engage in more flexible behaviour to afford learning of the task contingencies, over repeated, reinforced responding, solutions gradually come under the control of a system responsible for more automatic, goal-insensitive behaviour. This may serve to reduce the cognitive or computational demands of goal-oriented actions, which require holding in mind multiple representations of actions and outcomes, but at the expense of flexible responding as the individual is not 'thinking' about their behaviour. The interplay between habit formation and executive function processes (such as inhibition and working memory) in relation to chimpanzee behaviour is an important avenue of future research.

Another consideration, and avenue for research, is how the number of A trials administered affects error rate on the B trial. We have not systematically investigated this here, setting a minimum criterion of prepotency. However, Marcovitch and Zelazo (2006) found an 'inverted U shape' relationship between number of A trials and error response on the B trial in children: instead of the likelihood of error increasing in a liner fashion with A trials, it was found that a perseverative error was more likely to occur with a moderate number of A trials, but less likely when too few or too many A trials were administered. Marcovitch and Zelazo reasoned this may be because as A trials increase, children begin to consciously reflect on their decisions, affording improved performance on the B trial. This would be a fascinating area to explore comparatively with chimpanzees to determine if they, like children, show this pattern of response.

3.1 CONCLUSION

Inhibitory control is a vital component of behavioural flexibility. While this A not B task examined flexibility of search patterns in a relatively simple way, our results suggest that chimpanzees are likely to perseverate with a highly-practiced response in the face of a more optimal alternative. This draws parallels with research showing that chimpanzees will continue to use sub-optimal behaviours despite witnessing more productive (Hrubesch et al., 2009; Marshall-Pescini & Whiten 2008) or efficient alternatives (Davis et al., 2016). Although behavioural conservatism is often suggested to be explicable through low-fidelity copying of witnessed behaviours (Tennie, Call, & Tomasello, 2009), or suboptimal social learning heuristics (Dean et al., 2012), it may also be that conservatism arises through executive function processes, such as difficulties with inhibiting a well-established behaviour. Interestingly, here we found evidence of an order effect, where individuals performed worse on their second presentation of the A not B task (i.e. were more likely to make a perseverative search error on the B trial). This suggests that there was a lasting effect from the first task, with response prepotency to reach for A further heightened during the second presentation. Given that some cultural behaviours in chimpanzees are well-practiced solutions to foraging problems, which persist over time (e.g. Mercader et al., 2007), these results indicate that such behaviours may be particularly difficult to flexibly modify. We propose cognitive accounts of behavioural flexibility may help explain the relative stasis of chimpanzee culture.

CHAPTER 5: BIWAYS AND PITFALL

BEHAVIORAL CONSERVATISM IS LINKED TO COMPLEXITY OF BEHAVIOR IN CHIMPANZEES: IMPLICATIONS FOR COGNITION AND CUMULATIVE CULTURE

This manuscript is currently under review in Cognition

Sarah J. Davis[1,2], Steven J. Schapiro[2], Susan P. Lambeth[2], Lara A. Wood[3] Andrew Whiten[1]

ACKNOWLEDGEMENTS

I thank the care staff for their invaluable expertise and assistance throughout these projects and for the high standard of care and enrichment given to the chimpanzees, making this research possible. I are very grateful to Keith Haynes and Robert Mackenzie for the construction of the Pitfall box, Emma Flynn, Rachel Kendal and Andrew Long for the original design and construction of the Biways box, and William Nyberg for his technical and logistical support throughout these studies. I thank Cristine Legare, Richard Byrne, Eric Bowman, Gillian Vale and Stuart Watson for useful comments and suggestions throughout the project. This research was funded by the John Templeton Foundation (Grant ID: 40128, to K. Laland and A. Whiten). Support for the chimpanzee colony came from NIH U42 OD-011197.

COMPLIANCE WITH ETHICAL STANDARDS

Ethical approval was granted for this study by the UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee, and was carried out in accordance with approved guidelines.

[1]Centre for Social learning and Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, St Andrews, KY16 9JP, Scotland

[2]National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, the University of Texas MD Anderson Cancer Center, Bastrop, TX 78602, USA

[3]School of Social & Health Sciences, Abertay University, Dundee, DD1 1HG, Scotland

ABSTRACT

Cumulative culture is rare, if not altogether absent in non-human species. At the foundation of cumulative learning is the ability to flexibly modify, relinquish or build upon prior behaviors to make them more productive or efficient. Within the primate literature, a failure to optimize solutions in this way is often proposed to derive from low-fidelity copying of witnessed behaviors, sub-optimal social learning heuristics, or a lack of relevant socio-cognitive adaptations. However, humans can also be markedly inflexible in their behaviors, perseverating with, or becoming fixated on outdated or inappropriate responses. Humans show differential patterns of flexibility as a function of cognitive load, exhibiting difficulties with inhibiting sub-optimal behaviors when there are high demands on working memory. We present a series of studies on captive chimpanzees which indicate ape behavioral conservatism may be underlain by similar constraints; chimpanzees showed relatively little conservatism when behavioral optimization involved the inhibition of a well-established but simple solution, or the addition of a simple modification to a well-established but complex solution. In contrast, when behavioral optimization involved the inhibition of a well-established but complex solution, chimpanzees showed evidence of conservatism. We propose that conservatism is linked to behavioral complexity, potentially mediated by cognitive resource availability, and may be an important factor in the evolution of cumulative culture.

1. INTRODUCTION

Human culture is extraordinarily flexible in nature, exemplified by extensive diversification in technology and social practices. Behavioral flexibility forms not only the bedrock of this diversity but is a vital prerequisite for cumulative culture, affording the ability to build on established behaviors by modifying old solutions, and flexibly switching to more productive or efficient ones. Yet, our closest living relatives, chimpanzees, are reported to show difficulty in changing their solutions despite the availability of superior alternatives. Behavioral conservatism, whereby prior knowledge appears to block or delay adoption of an alternative behavior (Lehner, Burkart, & Schaik, 2011; Marshall-Pescini & Whiten, 2008), may help explain the relatively static and simple nature of chimpanzee culture.

1.1 BEHAVIORAL INFLEXIBILITY IN HUMANS AND CHIMPANZEES

Given the adaptive advantage of behavioral flexibility in solution optimization (convergence on the most productive or efficient behaviors), one might wonder why any species would exhibit highly conservative tendencies. Strikingly though, inflexibility in action or thought is well documented in human children (e.g. Carr et al., 2015; Defeyter & German, 2003; Jordan & Morton, 2012; Kirkham, Cruess, & Diamond, 2003; Zelazo, Müller, Frye, & Marcovitch, 2003), as well as in human adults (e.g. Bilalić, McLeod, & Gobet, 2008a; Bilalić, McLeod & Gobet, 2008b; Chrysikou et al., 2013; Diamond, 2005; German & Barrett, 2005; Gopnik, Griffiths, & Lucas, 2015; Luchins, 1942; Pope, Meguerditchian, Hopkins, & Fagot, 2015; Wiley, 1998). Within this human literature, the phenomenon is more often referred to in relation to concepts of perseveration, functional fixedness or mental set (aka *Einstellung*).

We suggest that perseveration analyzed in the human literature and behavioral conservatism described in the non-human primate literature, exhibit parallels: both involve the continued use of outdated responses despite knowledge of a more appropriate alternative. Typically, studies with humans involve explicit instructions about the benefits of adopting a new response (or costs of maintaining the old one), whereas non-human primate research often employs visual demonstrations of improved solutions. In contrast, functional fixedness, or mental set, tends to be more closely linked with (lack of) innovation, creative thinking, or insight, specifically getting 'stuck' on the common usage of a tool or behavior pattern, blocking solutions which would otherwise be easily generated (German and Defeyter, 2003), a blockage overcome once knowledge of an alternative becomes available.

There are several mechanisms which may account for a lack of behavioral change in chimpanzees (see Brosnan & Hopper, 2014; Dean, Vale, Laland, Flynn, & Kendal, 2013 for relevant reviews), such as low-fidelity copying (Lewis & Laland, 2012), or lack of relevant socio-cognitive adaptations (Tomasello, Carpenter, & Hobson, 2005). Here we examine behavioral conservatism, or perseveration with sub-optimal responses, by drawing from the human literature to advance a relatively unexplored cognitive account of why we observe behavioral inflexibility in our close primate cousins.

1.2 COGNITIVE ACCOUNTS OF BEHAVIORAL INFLEXIBILITY IN HUMANS

Changing behavior is a multi-faceted process, requiring attention to appropriate extrinsic or intrinsic cues indicating the costs/benefits of exploring alternative behaviors, the inhibition of the now outdated, inefficient or inappropriate response, and the ability to switch from this old response to a new one, which must be held in working memory (for a review see Bari & Robbins, 2013; Diamond, 2013).

Much research suggests that flexibility of response is affected by executive functions, and, in particular, links perseveration to two important factors: response pre-potency and working memory load (Grandjean & Collette, 2011; Roberts, Hager, & Heron, 1994; Roberts & Pennington, 1996). Extensive practice causes behavior to become a prepotent response, that is "reflexive actions, either innate or well established through a great deal of experience." (Miller, 2000), making it more difficult for this behavior to be subsequently relinquished through inhibitory processes (e.g. Crooks & McNeil, 2009). Research also highlights how increased demand on working memory may negatively impact on the learning of effective problem solving strategies (Beilock & Decaro, 2007; See also Gathercole et al., 2008).

Not only might these two factors affect behavioral flexibility, but they may also interact through shared neural and cognitive resources (Barber, Caffo, Pekar & Mostofsky, 2013; Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Chambers, Garavan, & Bellgrove, 2009 (for a review); Hester, Murphy, & Garavan, 2004; McNab et al., 2008; Mostofsky et al., 2003); for example, it has been found that increased demand on working memory creates greater difficulties in successfully inhibiting behaviors or adopting alternatives (Berger, 2004, 2010; Chmielewski, Mückschel, Stock, & Beste, 2015; Conway, Cowan, & Bunting, 2001; Davidson, Amso, Anderson, & Diamond, 2006; Grandjean & Collette, 2011; Hester & Garavan, 2005; Roberts et al., 1994; Stedron, Sahni, & Munakata, 2005; see also Kane & Engle, 2003; Marton, Kelmenson, & Pinkhasova, 2008; Redick, Calvo, Gay, & Engle, 2011). Taken together, these studies indicate

that the more complex the behaviors involved, the greater the difficulty in relinquishing an established response and adopting another, especially if an existing response is highly prepotent (Houghton and Tipper, 1994; Munakata, 2001).

1.3 COGNITIVE ACCOUNT OF BEHAVIORAL INFLEXIBILITY IN CHIMPANZEES

Increasingly, some studies do report a measure of behavioral flexibility in chimpanzees (Hopper, Kurtycz, Ross, & Bonnie, 2015; Manrique, Völter, & Call, 2013; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013), raising the prospect that behavioral conservatism may not explain the limited nature of chimpanzee culture. Such studies have often been reporting on only simple behavioral change, and initial behaviors which may not be considered as well-established or reliable solution strategies (e.g Horner & Whiten, 2005; Yamamoto, Humle, & Tanaka, 2013). However, chimpanzees appear to show difficulties in adopting, relinquishing and building upon behaviors when higher levels of complexity are involved (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016; Dean, Kendal, Schapiro, Thierry, & Laland, 2012; Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008). Interestingly, increased cognitive load, as in humans, has also been observed to affect behavioral optimization in chimpanzees (Evans, Perdue, & Beran, 2014; Seed, Call, Emery, & Clayton, 2009; see also Seed, Seddon, Greene, & Call, 2012), with perseverative responding in chimpanzees linked to human-like executive functions, namely, difficulties with inhibition (Vlamings, Hare, & Call, 2009; see also Beran, Washburn, & Rumbaugh, 2007). Given these findings, we propose that chimpanzee behavioral flexibility may be context dependent, with factors such as response pre-potency and complexity of behavior affecting the likelihood of behavioral change, and thence behavior optimization.

1.4 THE PRESENT STUDY

To explore the hypothesis that chimpanzee behavioral conservatism may be underlain by cognitive constraints similar to those demonstrated in human research, we presented captive chimpanzees with solution optimization puzzles. We first trained captive chimpanzees to adopt sub-optimal techniques. Solution optimization then required inhibiting these techniques to adopt a more productive alternative. One puzzlebox (the 'Biways box') involved only simple behaviors, whereas a second ('Pitfall box') involved a mixture of complex and simple solutions. We assumed that complex behaviors would be associated with a higher cognitive load, and thus expected chimpanzees to show greater difficulties with inhibition in that case.

There is no unitary concept of what makes one behavior complex and another simple, but we propose two metrics for which we might reasonably assume complexity. The first concerns

the learning of new behavioral processes; for example, individuals familiar with simple mechanics, such as levers, or sliding doors, do not need to relearn *how* to pull or slide when confronted with novel problems requiring these responses. They must only learn the particular affordances of the new problem and then apply known behaviors (Byrne & Russon, 1998). In contrast, solutions which require novel action elements must be learnt through some form of process learning. Therefore, in these studies, we class simple behaviors as those which are already well within the capabilities of the participants, and easily discovered by novices. Second, we might assume behaviors which require holding in memory several relations (or sources of variation) between objects, such as solutions involving multiple, non-arbitrary, steps, are more complex than behaviors which require fewer steps, with the former placing higher demands on cognitive resources (Halford, Wilson, & Phillips, 1998). As such, we consider these solutions, which are not easily adopted by novices, and which require relatively long periods of learning before mastery, as complex.

With a focus on the effects of solution complexity on behavioral flexibility, we aimed to answer the following questions:

I. Study 1.1 Biways box: Will chimpanzees relinquish an established but *simple* solution and switch to a *simple* alternative to increase reward pay-off?
II. Study 1.2. Biways box: Did having an established but *simple* solution hinder adoption of this *simple*, more productive alternative?
III. Study 2.1. Pitfall box: Will chimpanzees add a *simple* element on to an established but *complex* solution to increase reward payoff?
IV. Study 2.2. Pitfall box: Does having an established but *complex* solution hinder adoption of a *simple*, more productive alternative?

2. STUDY 1.1. Will Chimpanzees Relinquish An Established But *Simple* Solution And Switch To A *Simple* Alternative To Increase Reward Pay-Off?

2.1 STUDY 1.1 METHODS

The Biways box could be solved via use of one of two handles, which were distinguished by both location and coloring, as well as the action required to successfully operate them (Figure 1). Operating the top handle (slide handle) delivered one peanut, whereas the bottom handle (pull handle) delivered a higher value payoff, the peanut plus 2-3 grapes, the latter being a high value food reward for chimpanzees. Both methods were single-stepped and well within the

participant's repertoires. Accordingly, we denote these as relatively 'simple solutions': they do not require learning of new behavioral processes, or holding multiple relations in mind.

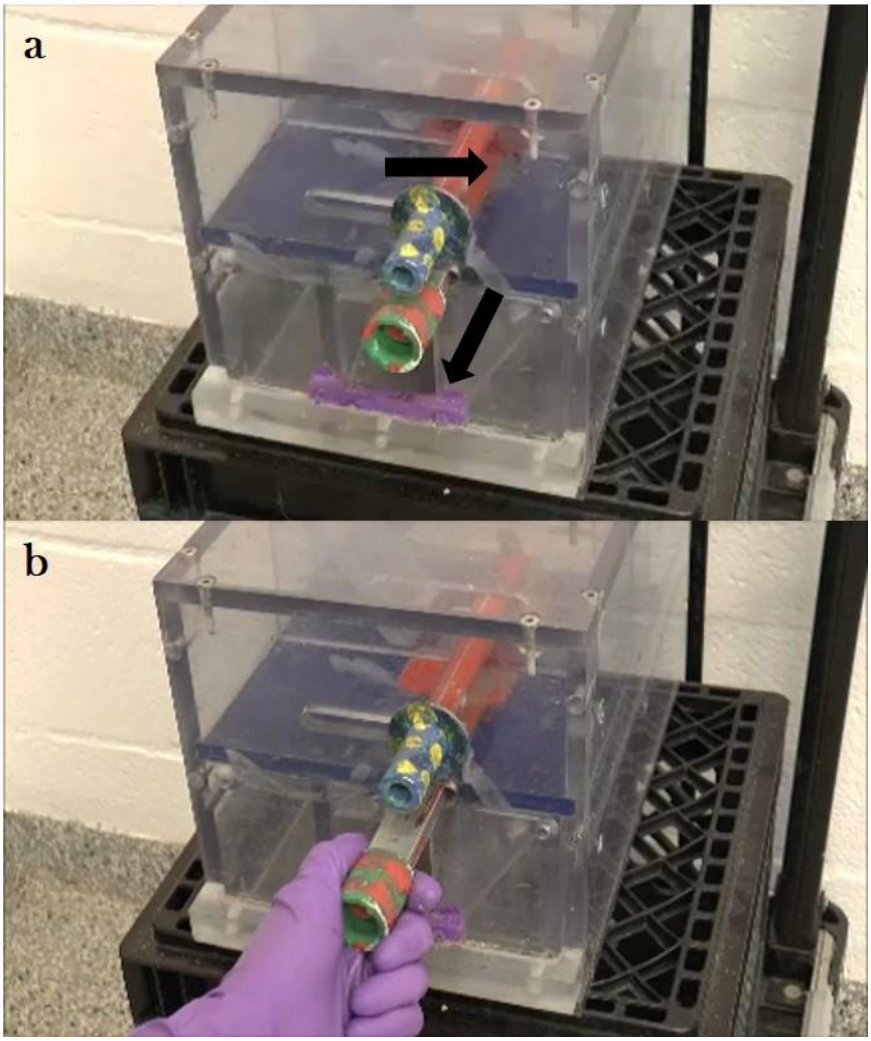


Fig. 1

The Biways box is shown in **a** and **b**. In **a**, the black arrows indicate the direction the handles can be moved, with the top handle slid to the right to produce the small reward, and the bottom handle pulled outwards to produce the larger reward, as shown in **b**.

Chimpanzees across five groups first learned the slide solution. In three of these groups, a conspecific model then demonstrated the more productive pull technique (Increased payoff with social information – IPSI – groups). In the remaining two groups, a model also introduced the pull technique, but the pull solution produced the same reward as the slide solution (i.e. there was no payoff incentive to change to this new technique – same payoff with social information – SI - groups). This was to determine if behavioral change was motivated by payoff.

Given the importance of social learning for the propagation, maintenance, and accumulation of culture (Boyd & Richerson, 1996; Legare & Nielsen, 2015), we examined the effects of social information on behavioral optimization through the inclusion of an asocial control condition. Here, individuals experienced the same puzzlebox configuration as the IPSI group, but no social information was available regarding the more productive pull technique (increased payoff but no social information - IP - individuals). Group conditions are summarized in Table 1.

Table 1
Group characteristics

Group	Group ID	Participants	Increased payoff	Social info
Increased payoff with social info	IPSI	8	Yes	Yes
Same payoff with social info	SI	6	No	Yes
Increased payoff but no social info	IP	5	Yes	No

Participants: Number of individuals in each group meeting criterion for inclusion; Increased payoff = Did the pull method result in a higher payoff than the slide handle? Social info = Was there social information available about the pull method?

Participants

Thirty-three chimpanzees participated (9 males; average age: 31.7 years; range: 13.09 – 50.39) and were group housed at the National Center for Chimpanzee Care at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop, Texas, U.S.A. See Appendix 3 Table S1 for further participant details.

Apparatus

The Biways box, originally designed for a comparative social learning study (Wood, Kendal, & Flynn, 2013), was re-purposed by SJD for the current study. It was transparent with the two handles protruding from the front. When the slide handle was slid to the right, it knocked a peanut off a shelf inside the apparatus, and down a chute, where it could be retrieved by the participant. Alternatively, the pull handle could be used to displace the entire shelf so that all of

the greater reward (nut + grapes) fell down the chute. The reward on the shelf was always visible to the participant.

Training phase

Increased payoff with social information (IPSI) groups (3 groups, N= 25) Groups received five hours of training where a trained, mid-high ranking, female conspecific demonstrated the slide solution to produce one peanut. The pull handle was locked so that it was immovable (thus making the grapes unobtainable). Participants were considered to have established the slide technique when they slid the handle fifty times over three separate training sessions, with no more than two touches to the pull handle (with the count reset at every third touch). Such a strict criterion ensured that not only was the slide solution a well-established response, but that any pull responses in subsequent testing were unlikely to be spurious, or 'accidental'. If an individual showed interest in participating, but was unable to complete training to criterion within the five hours, they were offered the opportunity to voluntarily enter their indoor enclosures and separate for further training.

Same payoff with social information (SI) group (2 groups, N= 13) Training followed that as outlined above, with the exception that the Biways box was baited with only one peanut.

Increased payoff but no social information (IP) group (N=5) Individuals were offered the opportunity to separate for training, with criterion for inclusion as outlined above. The box was baited with one peanut and three grapes, but only the peanut could be retrieved via sliding the handle. The pull handle was locked shut. Human demonstrations of the slide technique were given.

Testing phase

Increased payoff with social information (IPSI) group (3 groups, N=8) The pull handle was unlocked. Following model retraining, over ten hours of testing, the model now demonstrated the pull solution. Participants could thus solve the Biways box by sliding the slide handle (for one peanut) or could switch to pulling the more productive pull handle. When the participant removed the reward from the chute, the apparatus was immediately pulled away, reset and rebaited.

Same payoff with social information (SI) groups (2 groups, N=6) Testing followed the procedure above, with the exception that the pull handle resulted in the same reward as the slide handle (one peanut).

Increased payoff but no social information (IP) group (N=5) Testing was terminated after participants had completed 115 solutions. This number was chosen as this was more than 100 beyond the average number taken before switching in the IPSI group (median = 13.5), and exceeded the maximum number taken by any IPSI individual before switching to the pull handle (range of 1-114).

Coding and analyses

Training and testing phases were narrated and visually recorded using a HC-920 Panasonic camcorder, with responses coded through video analysis. A slide or pull behavior was coded when a participant manipulated only the slide or pull handle respectively. Manipulation of both handles was coded as 'both'. Convergence on the pull handle occurred when an individual used the pull technique on three consecutive occasions. Reversions were using the slide handle or both handles once a participant had switched to the pull technique.

Data were analyzed using Bayesian methods generated by the 'rethinking' package in R (McElreath, 2016), which was used for analyses throughout the studies reported. Appendix 3 describes the analyses in detail, and reports the results of alternative methods of statistical analyses, including a frequentist approach. Throughout analyses, a 95% confidence (or credible) interval is reported. This is the interval between which 95% of plausible values lie. The average value reported is the most probable of all these. Predictions generated by modelling procedures are also reported. These predictions are based off the sample data and attempt to capture population level behaviors. How much these predictions deviate from the sampled data is reported in Appendix 3. Model comparison techniques are also used to construct and choose between different models of the data. This involves inputting different combinations of parameters and seeing how well each predict the data in comparison to one another. We report here on the models which carry most of the Akaike weight (i.e. best predict the data).

Here, the model was fitted as the proportion of pull solutions out of the total number of responses (pull, slide and both), as predicted by the absence or presence of social information and higher payoff.

2.2 STUDY 1.1 RESULTS

Participant inclusion

Eight individuals in the IPSI groups met criterion for inclusion, six in the SI groups and five in the IP group.

Solutions used

In the IPSI groups, all chimpanzees switched to using pull on the median 14th solution attempt (range 1-114). During the transition of switching, individuals used both handles per solution a median of two times (range 0-9). There was little to no reversion to the original slide method, with only two individuals ever using the slide handle after switching (*Cr* used the slide method once in his subsequent 81 solutions, and *Cea* on three of her 84). Use of both handles per solution was rare post-switch (median = 2.4% of total post switch solutions, range = 0 - 4.8). In the SI groups, where the pull handle resulted in the same reward as the slide, four of the six individuals never manipulated the pull handle. *Chu* used the pull handle once on her first trial. *Ga* used both the pull handle and the slide handle, but with a strong preference for his original slide technique (sliding in 199/328 solutions). In the IP group, who had not witnessed a model perform the more productive pull solution, no individual discovered it. Testing data are summarized in Appendix 3 Table S2.

Regression model

The expected proportion of pull solutions for each group is summarized in Table 2 and Figure 2, with only IPSI groups predicted to use the pull solution (see Appendix 3 for further results). Results indicate a clear interaction effect of increased payoff and social information, with no important main effects of either factor alone.

Table 2

Proportion of expected pull responses for groups.

Information	Median	2.5%	97.5%
Payoff increase only (IP)	0	0	0
Social info only (SI)	0	0	0
Payoff increase and social info (IPSI)	0.81	0.55	0.99

The median is the expected median proportion of pull response, and 2.5% and 97.5% represent the 95% confidence intervals of the expected proportion.

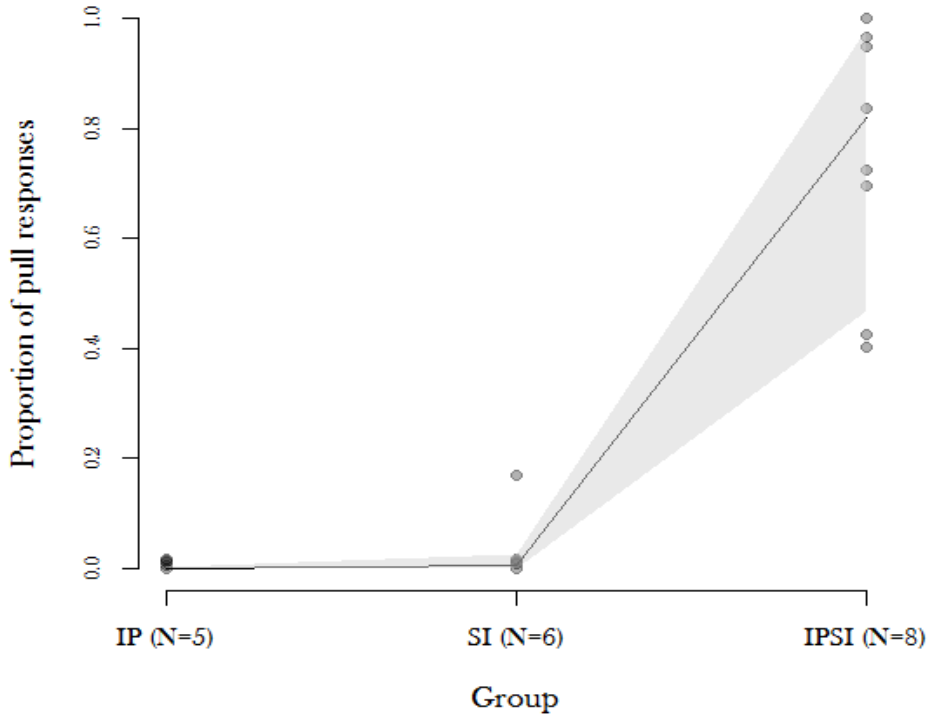


Fig. 2 Proportion of pull responses for individuals in the IP, SI and IPSI groups, with N number of participants shown for each group. The line is the mean of the predicted proportion of pull responses, with the shaded area showing 95% confidence intervals. The grey circles are the proportion of pulls for each participant based on their experienced conditions. These have been 'jittered' around the proportion value of zero for illustrative purposes.

2.3 STUDY 1.1 DISCUSSION

IPSI chimpanzees relinquished a highly established, but simple foraging behavior in favor of an alternative, simple solution. Comparison with the two other conditions showed chimpanzees required both a payoff incentive (cf Haun, Rekers, & Tomasello, 2014) and social information regarding the availability of this more productive alternative, in order to change their behavior. However, although there is a strong effect of social information, the lack of discovery in the asocial controls (IP individuals) is most likely due to an insight issue, not an inability to perform the pull technique; that is, participants likely just did not realize (and did not explore to discover) that the pull handle was an available solution. This suggests that having a highly practiced working solution may hinder exploration of alternatives (cf Bonawitz et al., 2011; Wood et al., 2013), and results are perhaps akin to functional fixedness or *Einstellung*. However,

when social information is available, this may be capitalized upon to encourage exploratory behavior, and more productive solutions thus subsequently found (Montague, King-Casas, & Cohen, 2006; Toelch, Bruce, Meeus, & Reader, 2011).

Most chimpanzees used both handles during any transition of switching to the pull technique. This may be a result of trial and error learning, or of some failure to completely inhibit use of the slide handle in the first instances of using the pull technique. Although reversion to using the slide handle was rare, participants occasionally employed use of both handles post-switch. The use of both handles during transition and reversions draws parallels with suggestions that children, when learning new problem solving strategies, have competing representations of these strategies, which overlap and compete not only during periods of transition, but over extended periods of time (Siegler, 1996).

While participants showed a ready ability to change their method of solution, it remained to be determined if having a well-established but simple prior solution hindered behavioral optimization through delaying convergence on the pull technique. It would appear this was the case for asocial control (IP) individuals but, as discussed above, this is perhaps due to a lack of exploratory behavior. In contrast, behavioral conservatism and perseveration are more often framed in conditions where individuals have knowledge of an alternative solution, and yet continue with an outdated or inappropriate response.

3. STUDY 1.2. Did Having An Established But Simple Solution Hinder Adoption Of The Simple, More Productive Alternative?

Although the previous study showed that chimpanzees could relinquish a sub-optimal behavior in favor of a more productive one, it was unclear if having a prior solution delayed behavioral optimization. In study 1.2, the numbers of solutions performed before converging on the more productive pull technique were compared between the IPSI individuals of study 1.1 and new, solution naïve participants: chimpanzees who had no prior, sub-optimal, solution to the Biways box.

3.1 STUDY 1.2 METHODS

Increased payoff but solution naïve (SN) groups (Groups=2, N=9).

The box was presented to two groups, with both the slide and pull solutions open to discovery, with the slide technique resulting in one peanut, and the pull producing one peanut plus 2-3 grapes. A high ranking model trained on the pull technique was present in each group.

Testing was terminated when participants had converged on the pull technique (pulling on three consecutive occasions)

Analysis

The number of attempts taken to converge on the optimum solution was compared between IPSI participants in Study 1.1 and SN individuals using a log-linear regression model. Further details on this model and addtitional analyses using Bayesian estimatation and frequentist methods are reported in the Appendix 3.

3.2 STUDY 1.2 RESULTS

It had taken a median of 13.5 (range 1-114) solutions for experienced individuals (IPSI group) to optimize their behaviour by using the pull solution, but a median of only 1 (range 1-43) solutions for naïve individuals. Analysis revealed that the lower limit of the 95% confidence interval of the effect of expereince with a prior, alternative solution was close to 0 (see Appendix 3). Naïve individuals were predicted to converge on the pull behavior a median of 10 solutions earlier (95% confidence interval 1-29; Table 3). However model comparison suggests having a prior solution may not have had a credible effect, as models with and without prior solution as a variable were given similar weight, i.e. describe the data almost equally as well (Appendix 3 Table S6). This indicates a potentially weak effect of having a prior solution. As analysis was conducted on a small sample size, alternative analyses were run (See Appendix 3) and did not change this conclusion.

Table 3
Model predictions

Knowledge	Median	2.5%	97.5%
Naive (SN)	3	1	6
Experienced (IPSI)	13	3	28

Median solution on which naïve and experienced individuals are expected to converge on the optimum solution, with 95% confidence interval

3.3 STUDY 1.2 DISCUSSION

Having a prior solution resulted in a predicted median of almost 10 more solutions to converge on the optimum behavior than those without a prior solution; however, this may not have credibly delayed behavioral optimization, with some expected overlap in the predicted behaviors of naïve and experienced individuals. This indicates that having a well-established, but

simple solution may nevertheless not have a strong impact on behavioral conservatism, or perseveration, with a well-known, but sub-optimal foraging behavior.

To further examine the causes of behavioral conservatism, the complexity of the initial solution was increased in study 2.

4. STUDY 2.1. Will Chimpanzees Add A Simple Element On To An Established But Complex Solution To Increase Reward Payoff?

As perseveration within the human literature is linked to cognitive load and solution complexity, chimpanzees were trained to extract a small reward from the Pitfall box described below, using a complex solution. Following this, a mid-high ranking, female conspecific introduced a simple addition to the solution, which improved productivity. Behavior was subsequently investigated over ten hours of testing. Unlike the Biways box, this solution involved a multi-stepped procedure, and was not one that could be readily discovered. In particular, chimpanzees showed difficulties in the learning of one novel action involving the removal of a defense block. Due to the incorporation of this novel element, and the multiple, non-arbitrary steps required, we propose that the initial solution for the Pitfall box was more complex than that needed for the Biways box.

4.1 STUDY 2.1 METHODS

Participants

Participants were group housed at the National Center for Chimpanzee Care (N=16, 4 males, mean =31.9 years, range: 19.8 – 50.9; demographics in Appendix 3 Table S7).

Apparatus

A transparent foodbox (Fig. 2) was structured on two levels, with a small reward on the top level (half a peanut) and a larger reward on the bottom (two peanuts). This was placed in the center of a large, transparent apparatus (Pitfall box; Fig. 2 – only the right side of the apparatus was used in these studies). This foodbox could be progressed along the Pitfall box using fingers via an open access slot on the front (from the chimpanzee's perspective). Three doors were located on the front of the apparatus (only Doors 1 and 2 were relevant to these studies), which could be opened to gain access to the reward within the foodbox. To progress the foodbox to Door 1, a block defense needed to be pushed out of the foodbox's path. A pit (or trap) was

located between this block and Door 1, which could be opened or closed by the experimenter (Fig. 2)

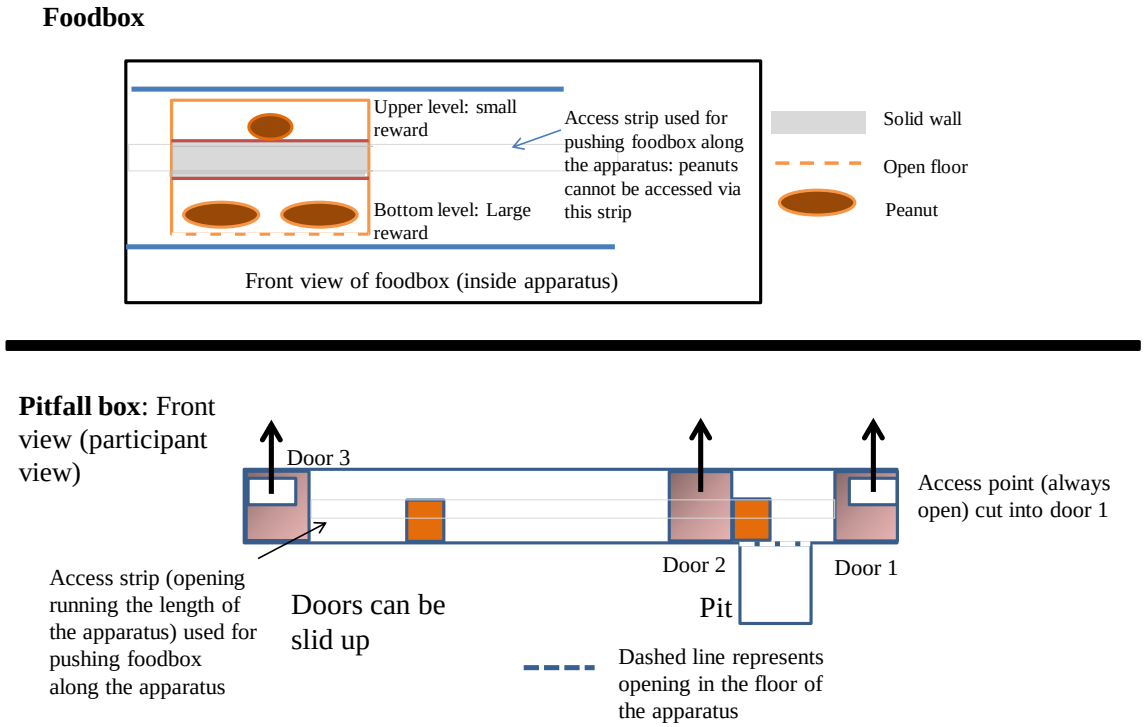


Fig 3 Foodbox and Pitfall box.

Training phase

Increased payoff with social information (IPSI) groups (Three groups, N=30) Chimpanzees were trained to solve the task by ferrying the foodbox to Door 1, removing the block defense along the way. At Door 1, the participant could reach in via a small access point cut into the door, and take the small reward from the top shelf of the foodbox. The large reward was in view, but was inaccessible as all doors were locked shut. Further, the pit was closed, and all food reward passed safely over (See Fig. 4 for details). Participants had to perform this solution 20 times to meet inclusion criterion.

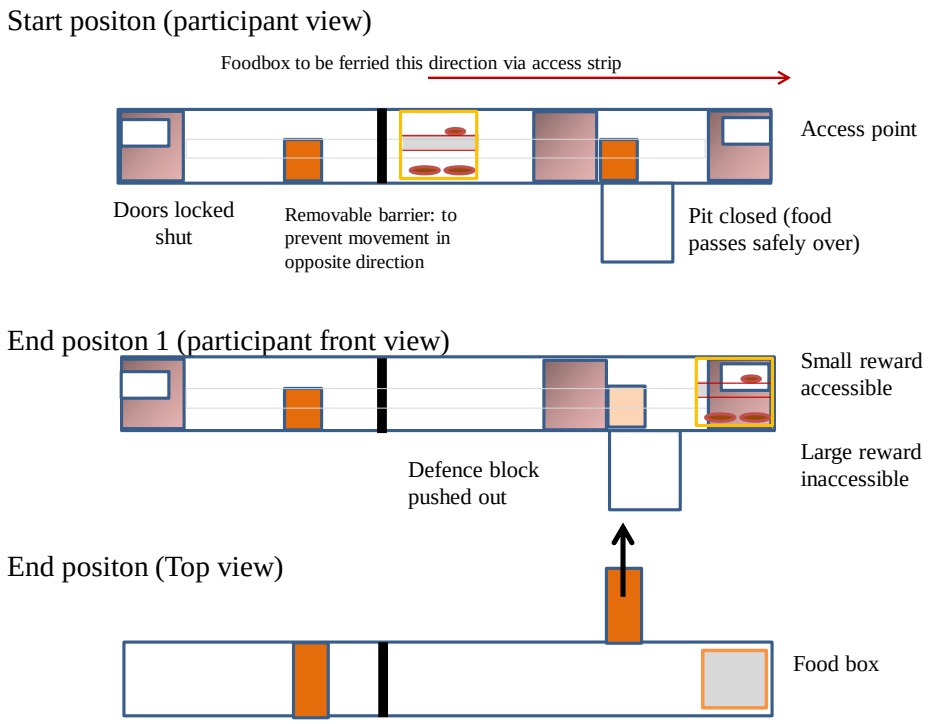


Fig 4. Trained solution to the Pitfall box

Initially, the designated model displayed this complex method over one hour of training; however, it became apparent that chimpanzees were finding it difficult to learn this solution, and in particular, the removal of the block defense. Removal required a hard 'poke' to the block, which caused it to shoot out the back of the apparatus. Many failed to perform this action, instead repeatedly pushing the foodbox against the block to no effect. To help solution acquisition, willing participants were given the opportunity to voluntarily separate for further human demonstrations and scaffolding of the solution. No verbal praise or reward was given for any part of the solution, other than the final retrieval of reward from the foodbox at Door 1. This ensured that particular elements of the solution were not themselves associated with some reward.

Once an individual had extracted the small reward, the apparatus was left against the mesh for a further 5 seconds. This extended time meant that there was opportunity to explore the apparatus in training, thus reducing spurious exploration in subsequent testing sessions

Increased payoff with no social information (IP) group (N=6) To examine the effect of social information on behavioral change, six individuals were offered the opportunity to

voluntarily separate for training, following the procedures above. If an individual did not wish to separate, they were trained in the presence of other group members, providing there was no interference by those individuals.

Testing phase

Increased payoff with social information (IPSI) group (N=10) Door 1 was unlocked. The model performed a new, more productive solution (Door 1 solution) in her group over ten hours of testing and open diffusion. This solution involved using the trained solution with the addition of pushing door 1 upwards, giving access to the previously inaccessible large reward (Fig. 5). Once the participant extracted any part of the reward, the apparatus was left against the mesh for 5 seconds, allowing further exploration and ensuring that failure to use Door 1 was not due to a lack of opportunity.

Increased payoff but no social information (IP) groups Individuals were offered the opportunity to separate for testing. Door 1 was unlocked and individuals were given up to one hour (over 20 minute sessions) to discover Door 1.

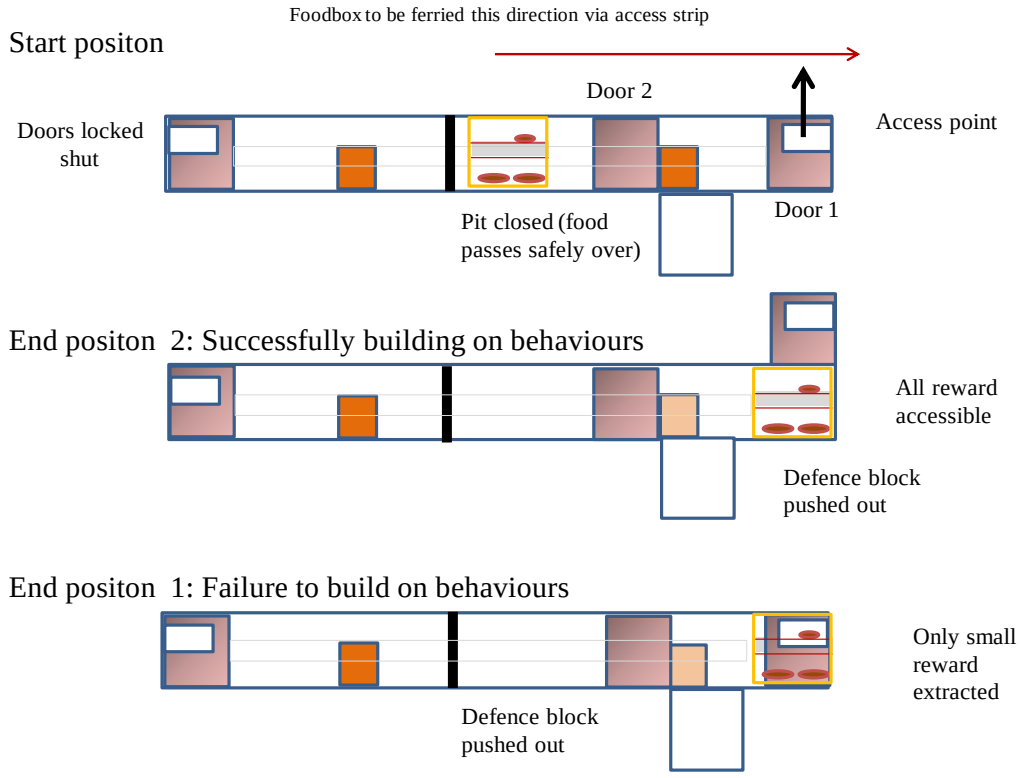


Fig 5. Door 1 solution

Analysis

To investigte the effect of social information on behavioral optimization, the number of attempts taken to converge on the optimum solution was compared between IPSI individuals and IP individuals, using a log-linear regression model. Further details on this model and addtitional analyses using Bayesian estimatation and frequentist methods are reported in Appendix 3.

4.2 STUDY 2.1 RESULTS

Participant inclusion

Ten individuals in the IPSI groups met criterion for inclusion, and six in the IP groups.

Solutions used

All chimpanzees in the IPSI groups quickly built on their behavior to improve productivity, doing so on their 3rd trial (median; range 1-24). Reversions to the trained solution were rare (median 0, range 0-2). Five participants in the IP groups (asocial controls) discovered door 1 (median attempts to discovery = 18.5, range 5-84).

Regression model: effect of social information

It was found that social information facilitated acquisition of the more productive solution by reducing the number of solutions taken to converge on the Door 1 solution (expected median of 12 trials earlier, 95% confidence interval of 3-33 trials earlier; Table 4), with a model including social information as a variable affecting optimization carrying almost all of the Akaike weight, thus describing the data better than a model without an effect of social information (see Appendix 3)

Table 4
Model predictions

Group	Median	2.5%	97.5%
IPSI/Social info	3	1	6
IP/No social info	17	5	33

Solution attempt on which individuals with (IPSI) and without (IP) social information are expected to converge on the optimum solution.

General flexibility

Chimpanzees employed variants of the same solution throughout testing, changing the order of the actions required for solution (Appendix 3 Table S10). Participants also pre-emptively removed defenses (the block and Door 1 - median of 8 number of pre-emptive moves, range 6-51).

4.3 STUDY 2.1 DISCUSSION

Little evidence of behavioral conservatism was seen on this task. Not only did chimpanzees in the IPSI groups readily build on their complex solution, but employed multiple variants of the same solution (see Appendix 3 Table S10), and often pre-emptively removed defenses to reward procurement. The accumulation witnessed here was very simple, involving a modification that was well within the behavioral repertoire of these chimpanzees, as demonstrated by asocial controls who also built on their solutions through individual discovery of Door 1. Social information facilitated acquisition of the more productive solution, but was not required for acquisition.

One reason for the lack of conservatism seen here may be due to the simplicity of the modification; that is, knowing a complex behavior may not result in behavioral conservatism when modification to solutions are simple and do not require learning of new behavioral processes. Another reason may be that chimpanzees were not required to inhibit a complex solution, as the Door 1 solution incorporated all elements of the trained solution. Human cognitive research has suggested that complex behaviors place a higher load on working memory, which interacts with inhibition processes (Diamond, 2013), potentially through 'using up' shared cognitive resources which may be required for successful inhibition. This results in perseverance with an outdated solution.

5. STUDY 2.2. Does Having An Established But Complex Solution Hinder Adoption Of A Simple, More Productive One?

To further examine potential causes of behavioral conservatism, and the interaction between solution complexity and inhibition, the apparatus was modified so that the pit was opened. This caused the large reward (but not the small one) to fall into the trap if the foodbox was progressed over this, as in the original Trained method and now extensively practiced Door 1 solution. Door 2 was unlocked and could now be opened to retrieve all reward. Hence, individuals in the IPSI groups could perseverate with their old solution, which would result in a

small reward, or they could inhibit their behaviors by not progressing the foodbox over the pit, and instead open Door 2 for all rewards. Door 2 was nearly identical to Door 1, which all participants had mastered in the previous testing session (study 2.1: median of 59 lifts, range 23-102).

The effect of social information on convergence on the Door 2 solution, and thus inhibition, was not examined here. The IPSI groups had ten hours of prior experience using the complex solution (Trained and Door 1 solutions), which would not have been possible with asocial controls, introducing a confound between the effect of social information and experience with the solution. We compared number of solutions taken by IPSI individuals against solution naïve chimpanzees (i.e. those with no prior knowledge of a sub-optimal solution) to converge on the Door 2 solution (evaluating the effect of prior solution on optimization). We also considered the number of solutions taken to converge on the Door 1 solution in Study 2.1 compared to the Door 2 solution here within IPSI individuals (looking at ease of incorporation of a simple modification to a solution when optimization requires building on, versus the inhibition of, a known solution).

5.1 STUDY 2.1 METHODS

Testing

Increased payoff with social information (IPSI) groups The Door 2 solution was displayed by the model during ten hours of testing and open diffusion (Fig. 6). Convergence on the Door 2 solution was taken as three consecutive Door 2 solutions, with little or no later use of alternative solutions.

Solution naïve (SN) group (Two groups, N = 8) A mid-high ranking, female conspecific was trained to display the Door 2 solution. Due to time constraints and monopolization of the apparatus by dominant individuals, groups had a 15 minute group-interaction period with the apparatus before interested participants were offered the opportunity to voluntarily separate (either on their own, or in small groups) until they converged on the Door 2 solution.

Analysis

To examine the effect of having a prior solution on behavior optimization, log-linear regression models compared the number of attempts taken to converge on the Door B solution between IPSI and SN groups, as well as between the number of solutions taken by IPSI individuals to converge on the Door 1 and Door 2 solutions (i.e. within subjects comparison).

Further details on these models and addtitional analyses using Bayesian estimation and frequentist methods are reported in the Appendix 3.

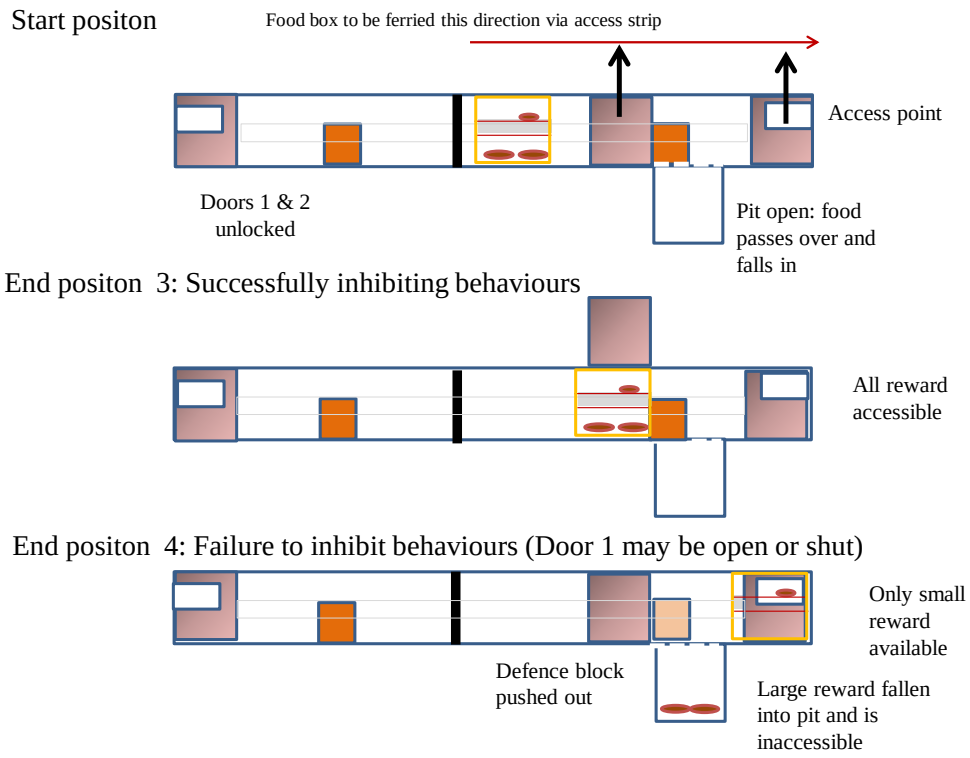


Fig 6. Door 2 solution

5.2 STUDY 2.1 RESULTS

Solutions used

IPSI participants used their old solution a median of 29.5 times (range 3 - 105) and the Door 2 solution a median of 51 times (range 0 - 90). Solution naïve individuals used only the Door 2 solution, apart from individual *Kg* who used the 'Trained' solution once, before discovering the Door 2 solution.

Reversions and redundant behaviors in IPSI individuals

The redundant lifting of Door 1, or removing the block when reward had already been extracted, were uncommon (median of 6 redundant actions, range 0-26). Reversions were also rare (median 4.5, range 0-8).

Regression model: Effect of prior solution

All IPSI chimpanzees, except individual *Ci,* converged on the optimum solution (median 28th solution, range 4 - 99), and naïve individuals on their median 1st solution (range 1-2).

Prior behavior credibly delayed adoption of the optimum behavior, with naïve individuals expected to take 14 fewer solution attempts (median, 95% confidence interval 8-24 fewer attempts; model predictions are presented in Table 5 and Figure 7). Model comparison gave all the Akaike weight to a model which included an effect of prior solution i.e. a model without prior solution as a factor does not adequately describe the data (see Appendix 3).

IPSI individuals are expected to take credibly more solutions (median 12, 95% confidence interval of 4 to 26) to converge on the Door 2 solution than the Door 1 solution of Study 2.1. Predictions are summarized in Table 6 and Figure 8.

Table 5
Model predictions

Group	Median	2.5%	97.5%
Naïve (SN)	1	1	2
Experienced (IPSI)	16	9	24

Solution on which individuals with (Experienced/IPSI) and without a prior solution (SN/Naive) are expected to converge on the optimum Door B solution.

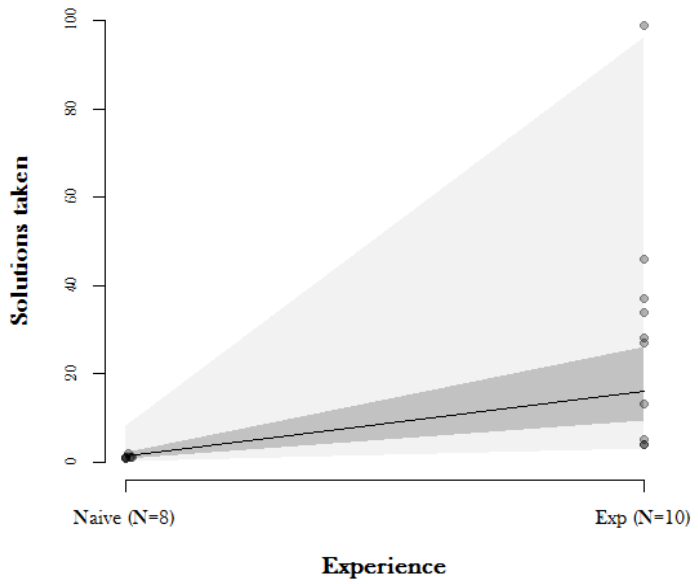


Fig 7. Model predictions for convergence on the optimum Door 2 solution for naïve and experienced participants. For Naïve individuals, points have been 'jittered' around the value of one for illustrative purposes.

Table 6
Model predictions

Solution	Median	2.5%	97.5%
Door 1	3	1	6
Door 2	16	7	27

Solution on which IPSI individuals are expected to converge on the optimum solution when they are building on a known solution (Door 1) versus inhibiting a known solution (Door 2).

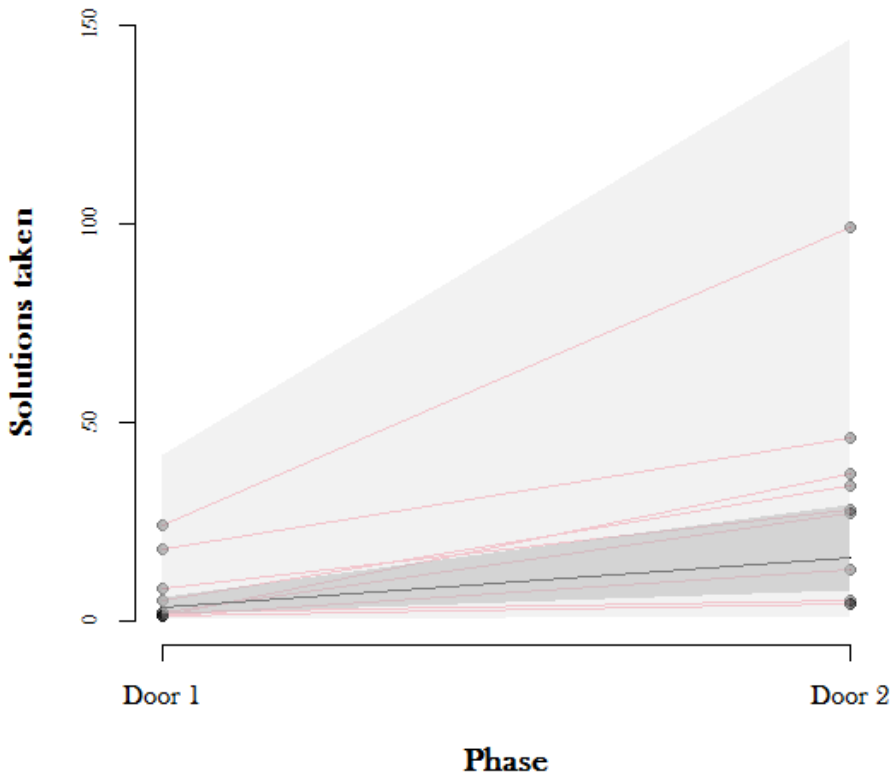


Fig 8. Model predictions for solution taken till convergence on Door 1 and 2 for IPSI individuals. Grey circles connected by thin pink lines represents the actual observed solution number on which an IPSI individual converged on Door 1 and 2 respectively.

6. BIWAYS AND PITFALL: SUMMARY

We do not directly compare the number of solutions taken by those with a prior, sub-optimal solution to converge on the optimum solution between the Biways and Pitfall participants. Although the manipulation of task complexity is our variable of interest, the effect of a prior solution can only be deduced from analysis that includes naïve individuals faced with the same task, rather than comparisons between tasks. In the Biways task, there is greater overlap in the predicted solutions taken until convergence between naïve and experienced individuals. There is no predicted overlap between these groups in the Pitfall task. In the Biways box, naïve chimpanzees (Biways-SN) did not converge on the optimum solution right away. This indicates that the behaviors seen in Biways-experienced individuals (Biways - IPSI) were perhaps similar to naive controls, and may not have been the result of perseveration. We cannot apply this reasoning to the Pitfall behaviors though, as the naïve individuals (Pitfall –SN) immediately converged on the optimum solution and so acted very differently from the experienced individuals (Pitfall – IPSI), who perseverated. We conclude there is a stronger and more credible effect of a *complex* prior solution.

7. GENERAL DISCUSSION

Chimpanzees showed relatively little conservatism when behavior optimization involved the inhibition of a well-established but simple solution (Study 1.2), or addition of a simple modification to a well-established but complex solution (Study 2.1). Such changes were facilitated by viewing a model perform the improved solution (Studies 1.1 and 2.1). In contrast, when behavioral optimization involved the inhibition of a well-established but complex solution, chimpanzees showed evidence of conservatism (Study 2.2). This was indicated by two separate findings:

I. Chimpanzees with a prior, sub-optimal solution (Pitfall -IPSI) took longer to converge on the optimum solution than chimpanzees who had no prior solution (Pitfall-SN); and

II. Chimpanzees with a prior, sub-optimal solution (Pitfall-IPSI) quickly optimized their established behaviors when optimization required the addition of a simple behavior, lifting a door (Door 1), to their original solution. However, when optimization again required the lifting of a door (Door 2), but the inhibition of the established solution, chimpanzees took longer to optimize their behavior.

Given that Door 1 and Door 2 were nearly identical, these findings cannot be explained by IPSI chimpanzees not recognizing the affordances of the apparatus, as they quickly converged

on opening Door 1 under the same conditions (with a pay-off incentive and social information). Nor can results be explained by chimpanzees not knowing *how* to open Door 2, as the opening process was the same as for Door 1, and readily discovered by solution-naïve chimpanzees. We therefore conclude that behavioral conservatism was caused in this case by a failure to inhibit a well-established solution. Further, given that chimpanzees did not show as strong an inability to inhibit their established solution when that solution was simple in nature (Study 1.2), we further propose that behavioral conservatism may be context dependent: behavioral conservatism is not due to an inhibition problem per se, but rather the inhibition of complex behaviors. Complex behaviors very likely place a higher demand on cognitive processes, such as working memory, which may limit the resources needed for inhibition. Thus, in line with human research, conservatism may be caused by limited cognitive resources. We suggest the consideration of task complexity may help account for the divergent findings within the primate literature on chimpanzees' behavioral flexibility.

7.1 HABIT FORMATION AND CHUNKING

As an alternative view, it could be that the original behaviors in both Biways and Pitfall were so well practiced that they became habitual. In habit formation, complex action sequences may be 'chunked' into a single executable unit, potentially reducing the cognitive resources needed to employ the solution, as the relationships between actions and outcomes do not have to be held in mind, so potentially more resilient to outcome dependent change (see Smith & Graybiel, 2014, 2016 for a review). Building on a chunked solution may not be as difficult as interrupting or changing the intrinsic contents of the chunk. In the Pitfall study 2.2, participants would have had to do just this: stop halfway along a chunked sequence and insert a new behavior, something they were not required to do in Biways or Pitfall study 2.1. This suggests that complexity of behavior affects behavioral optimization not because of limited cognitive resources per se, but rather because mechanisms such as chunking may reduce cognitive resource use by making complex behavior less computationally demanding.

Although we are not ruling out this alternative, we do suggest that the flexible use of multiple solution variants (Appendix 3 Table S10), as well as pre-dominant use of only outcome relevant actions, indicates that the participants may not have been on 'auto-pilot', but were goal-oriented in their behavior.

7.2 BEHAVIORAL COMPLEXITY AND CUMULATIVE CULTURE

Cultural behaviors, especially with regards to technologies like those of wild chimpanzees (Boesch, Head, & Robbins, 2009; Sanz, Schöning, & Morgan, 2010), can be complex in nature. Cumulative change in these behaviors typically involves an increase in complexity, and outside of our own hominin line, such cumulative complexity is rare. Our findings suggest that this may be caused in part by difficulties in relinquishing elements, or interrupting the sequence, of complex routines. Complementary work (Davis et al., 2016) has found that chimpanzees exhibit yet higher levels of behavioral conservatism when behavioral optimization involves not only the partial inhibition of a complex solution (mirroring Study 2.2), but also the addition of a complex element, as opposed to a simple one. In fact, most chimpanzees in the earlier Davis et al. study were able to build on this complex solution only by first mastering the additive element as an independent solution, and then combining this with their original, complex solution.

7.3 CONCLUSION

Notwithstanding other vital socio-cognitive adaptations, it is important to consider that whilst chimpanzees may possess some cognitive functions homologous with our own (Beran et al., 2016; Carruthers, 2013; Inoue & Matsuzawa, 2007; Manrique & Call, 2015; Martin-Ordas, Haun, Colmenares, & Call, 2010; Osvath, Kabadayi, & Jacobs, 2014; Osvath & Osvath, 2008; Vlamings et al., 2009), it is very likely that humans have a greater ability to hold on to and manipulate more information in working memory (Coolidge & Wynn, 2005; Haidle, 2010; see also Washburn, 2016). Thus, we can not only learn more complex sequences of behavior, but have more resources available to potentially facilitate behavioral flexibility.

Taken together, and in conjunction with previous research reviewed above, our results suggest that chimpanzees' conservatism is in part caused by complexities in the behaviors concerned, both when relinquishing such behaviors, or adding such behaviors to established ones, and this may be constrained by cognitive resource availability. We suggest that these behaviors are particularly relevant for cumulative culture, and may partially explain the relative stasis of chimpanzee compared to human culture.

CHAPTER 6: SERIALBOX

FOUNDATIONS OF CUMULATIVE CULTURE IN APES: IMPROVED FORAGING EFFICIENCY THROUGH RELINQUISHING AND COMBINING WITNESSED BEHAVIOURS IN CHIMPANZEES (*PAN TROGLODYTES*)

A version of this manuscript was published in Scientific Reports and included as Appendix 5

Sarah J. Davis[1, 2], Gillian L. Vale[1, 2], Steven J. Schapiro[2], Susan P. Lambeth[2], Andrew Whiten[1]

ACKNOWLEDGEMENTS

I thank the care staff for their invaluable expertise and assistance throughout the project and for the high standard of care and enrichment given to the chimpanzees, making this research possible. I am very grateful to Keith Haynes and Robert Mackenzie for the construction of the Serialbox and for designing Fig. 1, and William Nyberg for his technical and logistical support throughout this study. I thank Lisa Reamer for her advice and suggestion to use a token reward, Stuart Watson for providing interrater reliability and Richard Byrne for his constructive feedback on an earlier version of this manuscript. This research was funded by the John Templeton Foundation (Grant ID: 40128, to K. Laland and A. Whiten). Support for the chimpanzee colony came from NIH U42 OD-011197.

COMPLIANCE WITH ETHICAL STANDARDS

Ethical approval was granted for this study by the UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee, and was carried out in accordance with approved guidelines.

[1]Centre for Social learning and Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, St Andrews, KY16 9JP, Scotland

[2]National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, the University of Texas MD Anderson Cancer Center, Bastrop, TX 78602, USA

ABSTRACT

A vital prerequisite for cumulative culture, a phenomenon often asserted to be unique to humans, is the ability to modify behaviour and flexibly switch to more productive or efficient alternatives. Here, we first established an inefficient solution to a foraging task in five captive chimpanzee groups (N = 19). Three groups subsequently witnessed a conspecific using an alternative, more efficient, solution. When participants could successfully forage with their established behaviours, most individuals did not switch to this more efficient technique; however, when their foraging method became substantially less efficient, nine chimpanzees with socially-acquired information (four of whom witnessed additional human demonstrations) relinquished their old behaviour in favour of the more efficient one. Only a single chimpanzee in control groups, who had not witnessed a knowledgeable model, discovered this. Individuals who switched were later able to combine components of their two learned techniques to produce a more efficient solution than their extensively used, original foraging method. These results suggest that, although chimpanzees show a considerable degree of conservatism, they also have an ability to combine independent behaviours to produce efficient compound action sequences; one of the foundational abilities (or candidate mechanisms) for human cumulative culture.

1. INTRODUCTION

Culture has been defined as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (Laland and Hoppitt 2003 pg 151), The ability to build upon or ratchet up on such cultural behaviours, creating cumulative cultural change (Tomasello, Kruger & Ratner, 1993), can lead to substantial gains in productivity or efficiency, well exemplified in its elaboration in humans (Boyd & Richerson, 1996). Whilst the ability to socially learn behaviours (defined as "learning that is influenced by observation of, or interaction with another animal (typically a conspecific) or its products" (Heyes 1994, pg 207) may be common across many animal taxa (Heyes & Galef, 1996; Hoppitt & Laland, 2013; Galef & Whiten, 2017; Reader and Biro, 2010; Zentall & Galef, 1998), cumulative culture is limited or, according to some authors, absent in non-human animals (Boyd and Richerson 1996; Tennie et al., 2009; Tomasello et al., 1993). This is most striking when we compare our human cultures with those of arguably the second most cultural species, our closest living relative, the chimpanzee (*Pan troglodytes*) (A Whiten et al., 1999).

Chimpanzees exhibit the greatest number of traditions outside of the human species, across foraging, tool use and social behaviours, with each chimpanzee group distinguished by their own particular cultural profile (Whiten et al., 1999). Yet, there is little evidence for cultural accumulation on these traditions (see Dean et al., 2013). Various factors may contribute to the stasis of chimpanzee culture, such as relevant socio-cognitive adaptations (Dean, Kendal, Schapiro, Thierry, & Laland, 2012), low fidelity social learning mechanisms (Call, Carpenter, & Tomasello, 2005), or failure to employ appropriate learning heuristics (Laland, 2004; Marshall-Pescini & Whiten, 2008). However, cumulative culture ultimately requires the ability to change established behaviours in order to adopt more efficient or productive ones; that is, in order to upgrade solutions, an individual must possess the behavioural flexibility to relinquish, modify and build on prior solutions. Behavioural inflexibility may therefore, in and of itself, limit the evolution of culture. With behavioural flexibility defined as "the continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution" (Lehner et al., 2011, pg 447), a lack of such flexibility has been found in several experiments with chimpanzees. Marshall-Pescini and Whiten[16] found that young chimpanzees failed to cumulatively modify their foraging efforts by building on their exisiting behaviours despite witnessing a more productive solution. Yet, the more complex behaviour could be acquired if participants had no prior knowledge of the less lucrative foraging technique. This led the authors to suggest that chimpanzees are behaviourally conservative, since

reported in several further studies (Hrubesch et al., 2009; Price et al., 2009; Hopper et al., 2011; Dean et al., 2012; Bonnie et al., 2012; see also Haun et al., 2013) in simple terms, chimpanzees tend to become 'stuck' on known behaviours despite availability of superior alternatives.

These results appear inconsistent with other findings such as that of Horner and Whiten (2005), where chimpanzees 'streamlined' their behaviours after witnessing inefficient options used by others. However, this involved omitting elements (Flynn, 2008; Tennie et al., 2009a), as opposed to the additive, ratchet effect required for cumulative culture (Boyd & Richerson, 1996) . Similarly, following social demonstrations in a juice acquiring task, Yamamoto, Humle and Tanaka (2013) found that chimpanzees switched from using a straw as a dipping tool to exploiting a more efficient sucking function, but this also did not involve additive ratcheting. Such findings are in line with records of behavioural modification in the wild (Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Luncz, Wittig, & Boesch, 2015; Sirianni, Mundry, & Boesch, 2015; Stokes & Byrne, 2001; Wilfried & Yamagiwa, 2014; see also Hockings et al., 2015), as well as more recent experiments demonstrating payoff-related variation in simple behaviour, such as depositing 'tokens' in novel locations to increase food reward value (Hopper, Kurtycz, Ross, & Bonnie, 2015; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013).

From studies examining behavioural change in humans, we might expect at least two factors to have differential effects on behavioural flexibility: the extent to which behaviour has been practiced, and the complexity of the behaviour involved (Grandjean & Collette, 2011; Roberts, Hager, & Heron, 1994; Roberts & Pennington, 1996). As cultural traditions are often well-established and long-held behaviours, and are also sufficiently complex to necessitate social learning to acquire them, it may be important to consider how well-ingrained the behaviour to be modified is when extrapolating results to chimpanzees' potential for cumulative culture. Evidence now exists that chimpanzees can recognise and adopt superior variants of behaviours which are simple and conceptually similar to existing routines (Hopper et al., 2015; Van Leeuwen, et al., 2013). Chimpanzees can also relinquish old solutions and build on very simple behaviours to form action sequences when these sequences are within most chimpanzees' repertoires (Manrique, Völter, & Call, 2013), as well as relinquish behaviours that have been performed but not yet adopted as a reliable foraging strategy (Horner & Whiten, 2005; Yamamoto et al., 2013). However, the extent to which chimpanzees can modify, relinquish or build-upon well-established, cognitively more complex behaviours, those that perhaps mirror cultural behaviours more closely, remains to be established (Dean et al., 2012; Marshall-Pescini & Whiten, 2008).

In the present studies, we investigated chimpanzees' ability to build upon socially acquired, complex behaviour in the context of improving efficiency. Of particular interest is whether a chimpanzee can benefit by witnessing a more efficient behaviour used by a conspecific compared to one they currently reliably employ to achieve the same goal, and flexibly switch to using this more efficient behaviour.

A transparent puzzle box (Fig. 1) was used (hereafter 'Serialbox') from which a valued token could be extracted (later exchanged for a food reward) via either of two alternative operations differing in efficiency, with the inefficient method more labour intensive and taking longer to complete. The efficient method involved partial use of behaviours common to the inefficient method, along with the addition of a novel behaviour. The efficient method therefore involved not only streamlining the inefficient method by a *subtractive* process (noted in some studies of cumulative culture (Flynn 2008; Tennie, Walter, Gampe, Carpenter, & Tomasello, 2014), but also the *addition* of a novel behavioural element to an established sequence, that is, a ratcheting up on behaviour[2]. Participants across five groups were initially trained to extract a valued token from the transparent Serialbox via a multi-stepped, repetitive, inefficient process (Fig. 1). To strengthen ecological validity when assessing chimpanzees' cumulative cultural capabilities, this extraction process was completed a minimum of 20 times over several sessions until it became a reliable and ingrained response. Three groups ('social information' groups) subsequently witnessed a conspecific model using the more efficient, solution described in Fig. 1 and more fully in Methods below. Following repeated social demonstrations, the behaviour of participants was examined over ten hours of open diffusion, monitoring any spread of the more efficient technique, to better simulate the diffusion of behaviours in a culturally relevant context (Whiten & Mesoudi, 2008).

We hypothesised that if chimpanzees could recognise a solution more efficient than the one they were currently employing and were able to switch to this, they should do so once they witnessed the actions of the model, regarded as a simulated 'innovator' (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). To assess how readily chimpanzees could themselves innovate and switch to the efficient method without the need for social information, we trained two control groups to use the inefficient method but did not expose them to the efficient method through a trained conspecific ('non-seeded' groups). To investigate how naïve chimpanzees might solve this extractive problem when they did not have an established solution to the puzzle, the Serialbox was introduced to one additional control group who were not initially trained to extract

via the inefficient method ('naïve' group). For this group, the problem could be solved by using either the efficient or inefficient strategy.

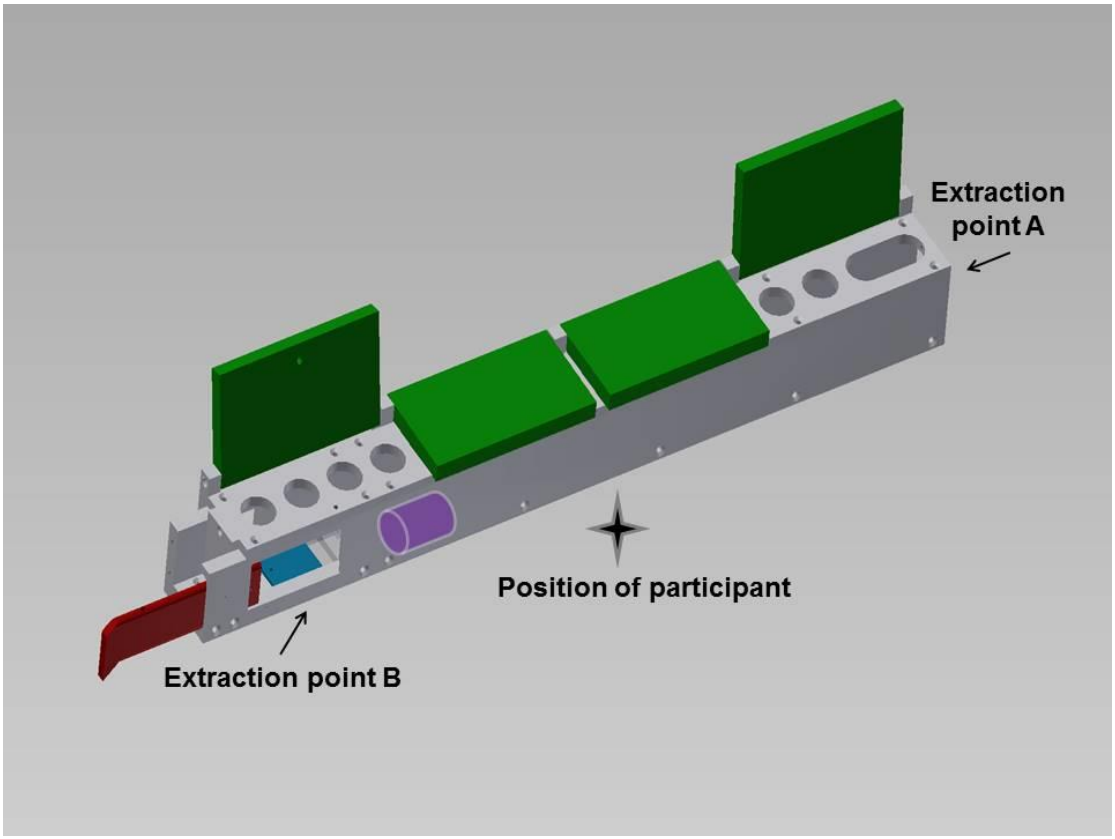


Figure 1. Serialbox. Along the length of the transparent Serialbox were four compartments. Each compartment had a hinged lid on top which could be lifted open (coloured here in green for image clarity; in reality all parts were transparent). Under each lid were four finger holes that permitted an object (depicted as a purple cylinder) initially provisioned in the left-most compartment to be pushed the length of the apparatus. This object could then be extracted through an opening at the other end ('Extraction point A'). This was the inefficient method in Experiments 1 and 3. A small door spanning two thirds of the first compartment (coloured here in red for clarity) was fitted on the chimpanzee side of the apparatus and could be pulled open using a handle protruding from the outside of the box to give alternative and quicker access to the left-most compartment ('Extraction point B'), where the token was initially positioned. This, in combination with lifting the lid of the left-most compartment and using the underlying holes to manoeuvre the token to extraction point B, was the efficient method in Experiments 1 and 3. The blue square shown in the left-most compartment depicts the indent in the floor in which the token was placed throughout Experiment 2.

2. EXPERIMENT 1: RELINQUISHING AN INEFFICIENT SOLUTION

2.1 EXPERIMENT 1: METHODS

Table 1.
Participant Demographics meeting criterion for inclusion

Individual	Sex	Age	Group	Wild/captive	Rearing
My	F	49.26	Model	Wild	Unknown
Ma	F	48.26	Social info	Wild	Unknown
Cea	F	23.10	Social info	Captive	Mother
Ze	F	11.95	Social info	Captive	Mother
Ta	F	21.36	Social info	Captive	Mother
Co	F	30.24	Model	Captive	Mother
Se	F	15.40	Social info	Captive	Mother
Hh	F	23.93	Social info	Captive	Mother
Cr	M	18.78	Social info	Captive	Mother
An	M	22.86	Social info	Captive	Mother
Mi	F	24.69	Model	Captive	Mother
Sa	F	24.71	Social info	Captive	Mother
Je	F	24.96	Social info	Captive	Mother
Si	M	24.74	Social info	Captive	Mother
Kt	F	25.78	Non-seed	Captive	Nursery
Na	F	23.88	Non-seed	Captive	Nursery
Ae	F	39.39	Non-seed	Wild	Unknown
Ai	F	19.21	Non-seed	Captive	Nursery
Gs	M	22.41	Non-seed	Captive	Nursery
Chu	F	33.57	Non-seed	Captive	Mother
Sha	F	23.75	Non-seed	Captive	Mother
Ka	F	23.56	Non-seed	Captive	Mother
Jy	M	42.52	Naïve	Wild	Unknown
Ua	F	50.53	Naïve	Wild	Unknown
Cy	M	24.41	Naïve	Captive	Mother
Zy	M	43.52	Naïve	Wild	Unknown
Ha	F	48.53	Naïve	Wild	Unknown

From left to right: Individual: Initials of participant (individuals are organised by their groups with participants listed under their respective models); Sex: F = female, M = male; Age: Age in years at time of testing; Group: Social info = social information group; Non seed = non-seeded; Naïve = Naïve group; Captive/wild: Captive = born in captivity, Wild = born in the wild; Rearing: Mother = raised by mother, Nursery = raised by human caretakers.

N = 43 individuals (18 males; average age: 29.1; range: 11.9 -50.5 years; Table 1) were group housed at the National Center for Chimpanzee Care Individuals were given the opportunity to voluntarily participate and separate from their group for further training and testing purposes in their inside enclosures for a period of no longer than 30 minutes. Participants were not food or water deprived during training or testing.

Apparatus

A transparent, elongated, Plexiglas 'Serialbox', measuring 61 centimetres long, five centimetres high and five centimetres wide, was attached to a mobile cart and pushed to the mesh of enclosures. Along the length of the transparent Serialbox were four compartments (Fig. 1). Each compartment had a hinged lid on top which could be lifted open. Under each lid were four finger holes (2.5cm in diameter) that permitted an object initially placed inside the box at the left-most end from the chimpanzees' perspective to be pushed the length of the apparatus. This object could then be extracted through an opening at the other end of the Serialbox ('Extraction point A' in Fig. 1). A small door spanning two thirds of the first compartment was fitted on the chimpanzee side of the apparatus and could be pulled open using a handle protruding outside the box to give alternative and quicker access to the left-most compartment ('Extraction point B' in Fig. 1), where the token was initially positioned.

Procedure

Training phase (5 groups, 38 chimpanzees)

Chimpanzees were initially trained to associate a small purple plastic token with a reward by trading this with experimenter SJD in exchange for one grape. The token was then placed inside the apparatus three quarters of the way along the first compartment (Fig. 1). The inefficient method of retrieving the token was demonstrated by SJD three times before participants interacted with the Serialbox. The inefficient method involved the lifting of each of the lids of the four compartments providing access to the finger holes. These holes were used to ferry the token along the compartments of the apparatus until it could be extracted from point A.

Following these demonstrations, the box was pushed to the mesh allowing all individuals in each group access. Once the token was extracted from the apparatus, it was exchanged with SJD for one grape. During the training phase, the efficient method was not available because the pull door was locked shut, preventing extraction from point B. If an individual was not able to successfully retrieve the token after demonstrations, scaffolding of the solution was provided whereby the token was positioned adjacent to extraction point A until extraction from this point was mastered, with additional demonstrations given if necessary. The token was gradually placed further away until the chimpanzee was manoeuvring the token along the length of the apparatus by opening the lids and using the underlying finger holes. Participants were given the opportunity to engage with the Serialbox until all participating individuals had successfully retrieved the token a minimum of twenty times over no fewer than two training sessions. When an individual was successful in retrieving the token, the apparatus was pulled back from the mesh, reset and re-baited. If an individual showed interest in operating the apparatus but was unable to gain access due to monopolisation by more dominant individuals, they were offered the opportunity to voluntarily enter their indoor enclosures and participate by themselves until they had reached criterion for inclusion in the study.

Social information groups: Presence of social demonstrator (Three groups, N = 26)

Model training phase. After all participating chimpanzees had reached criterion, a high ranking female chimpanzee voluntarily separated from her group and was trained on how to open the Serialbox using a more efficient method. This involved pulling the door open, and, due to the positioning of the token a short distance from the extraction point (Fig. 1), lifting one lid and using the underlying finger holes to manoeuvre the token towards point B for efficient retrieval. Training sessions lasted around twenty minutes.

Social demonstration phase. The Serialbox was re-introduced to the entire group with the efficient method no longer locked. The token could now be retrieved via either extraction point A or B. The model was called by name and vocally encouraged to demonstrate the efficient method, which all models complied with. Following each extraction, the token was exchanged with SJD for one grape. After each participant had witnessed at least ten demonstrations of the more efficient method over no fewer than two separate testing sessions, the entire group was given the opportunity to interact with the Serialbox. A demonstration was taken to occur if an individual was within two metres of the model and the potential observer's head was orientated towards the apparatus. If a participating individual did not come into proximity with the model

during the social demonstration phase, they were given the opportunity to voluntarily separate with the model and observe her actions. After the model had successfully retrieved the token, the apparatus was pulled away from the demonstrator, reset and re-baited.

Testing phase (N = 11). The apparatus was presented over ten hours to all participating individuals with both the efficient and inefficient methods as viable strategies to extract the token. After each successful extraction, the apparatus was pulled away, reset and re-baited. To avoid cueing of responses, SJD occluded the apparatus and her hand movements with a sheet during interactions with the box. The apparatus was not made available to any non-participating chimpanzee (i.e. any individual who had not met criterion to be included in the study).

Non-seeded groups: No social demonstrator (Two groups, N = 12)

Control groups experienced the Training phase and Testing phase as above, but no model seeded knowledge of the more efficient method.

Naïve group (1 group, N = 5 chimpanzees)

This control group was exposed to the apparatus with no prior knowledge of any solution over ten hours of open diffusion. Both the efficient and inefficient methods were viable extraction techniques.

Analyses

Records of the social demonstration and testing phases were both narrated and visually recorded using a HC-920 Panasonic camcorder. Responses were coded in situ for all groups, with 'social information' groups' behaviour additionally coded through video analysis.

2.2 EXPERIMENT 1: RESULTS

Due to limited sample sizes, data were analysed using non-parametric methods with exact P values reported. Effect sizes were calculated using the Z score of the test statistic such that $r = Z/\sqrt{N}$, where N was the total number of observations included in the analysis. An analysis of interrater reliability using Cohen's kappa found excellent agreement ($\kappa = 1$) between two coders' judgement of whether the participant was extracting via the inefficient or the efficient method.

Participant inclusion and extractions across training and test phase

Eleven individuals in the 'social information' groups and eight in 'non-seeded' control groups met criterion for inclusion in the study (a minimum of 20 inefficient extractions; see Table 1 for participant demographics; Appendix 4 Table S1 for behaviours in the training and test periods; Appendix 4 Table S2 for relative efficiency of the two extraction techniques). There was no difference in the acquisition of the inefficient method between the 'social information' and 'non-seeded' individuals in terms of number of extractions made during the training period (Mann Whitney $U = 36$, $P = .529$; Appendix 4 Table S1).

Within the 'social information' groups, to analyse any growing behavioural proficiency, the mean time taken across the first ten extractions using the inefficient method were compared to the mean time taken across the last ten inefficient extractions, using a one-tailed Wilcoxon signed rank test. If an individual did not extract 20 times during the testing period, the mean time taken for inefficient extractions either side of the median extraction were calculated and compared. Individuals became significantly more proficient at the inefficient method over this test period ($Z = -2.803$, $n = 10$, $P = 0.001$, $r = -0.63$), with a median reduction in extraction latency from 47.5 to 26.2 seconds.

Switching behaviours

Across this testing period ('E1'), nine of the 11 individuals in the 'social information' groups and all individuals in the 'non-seeded' groups continued to exclusively use the inefficient method established during the training period ('E0') to extract the token.

To test for switching behaviour at the individual level, following van Leeuwen et al. (2013), the number of inefficient and efficient extractions performed during E0 and E1 were compared using a one-tailed Fisher's exact test. Two individuals (from separate groups) demonstrated a significant change of behaviour within this period, switching to using the efficient solution (Individual *Se*: $E0_{0,21}$, $E1_{10,16}$, $P = .001$; Individual *Sa*: $E0_{0,22}$, $E1_{179,0}$, $P < 0.0001$: subscripts represent frequencies of efficient and inefficient methods respectively).

'Naïve' group

One individual, *Jy,* discovered and used the efficient method within two hours of interaction with the Serialbox. Individual *Ua* observed *Jy*'s efficient method five times; following three initial failed attempts to open the door, she successfully used the efficient method to extract the token in a subsequent test session. Before *Ua* witnessed use of the efficient method, she had unsuccessfully interacted with the apparatus, exploring only the holes and lids. Two other

individuals witnessed the use of the efficient method just one and five times each and never successfully extracted the token. There was no discovery of the elaborate, inefficient method.

2.3 EXPERIMENT 1: DISCUSSION

When chimpanzees used a well-established but laborious solution to successfully gain rewards, most were not seen to further explore alternatives, or to capitalise on social information available about a more efficient approach. The central finding from Experiment 1 was thus of a remarkable degree of conservatism, expressed in perseverance with a well-rehearsed routine despite witnessing a more efficient alternative modelled by another chimpanzee. Such conservatism has been documented in a series of other recent chimpanzee studies (Bonnie et al., 2012; Dean et al., 2012; Hopper et al., 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009). By contrast, in the 'naïve' group, the efficient method was discovered, if by only a single persistent individual, and was later adopted by another chimpanzee. The results thus tentatively suggest that having a prior solution may in itself hinder adoption of a superior alternative (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). Such conservatism may have some adaptive value insofar as switching to an alternative may be costly, either through cognitive demands inherent to learning or potential loss of reward through lack of expertise in this method (Cohen, McClure, & Yu, 2007; Reader & Laland, 2003). In fact, chimpanzees, who at the start of the testing period were already well practiced at the inefficient method, effectively halved the time taken to successfully extract the token across the testing period. This indicates growing expertise and skill proficiency in their behaviour, and supports previous findings that skill mastery may hinder behavioural change (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008).

To further investigate the limits of behavioural conservatism, in Experiment 2 the disparity in efficiency of behaviours was increased such that the inefficient method became not only an unreliable means of foraging but even when successfully employed, the latency to extraction from point A was typically far higher than for B. In addition, the alternative behaviour needed for extraction at point B was reduced to a single element and did not require use of parts of the inefficient method, so subjects had only to relinquish an established solution and adopt a novel one-stepped alternative with no ratcheting on prior behaviours.

3. EXPERIMENT 2: RELINQUISHING A HIGHLY INEFFICIENT SOLUTION

The movement of the token along the length of the apparatus to extraction point A was impeded by placing the token in an indentation in the floor, directly behind extraction point B (Fig. 1), so movement of the token towards A was more awkward to initiate. However, the token could now be extracted from point B solely by just pulling the door open. Raising lids and using finger holes was unnecessary. Accordingly, this experimental manipulation made the inefficient method more so, and the efficient method yet easier, enhancing the contrast between them (Appendix 4 Table S2).

The 19 subjects who had met criterion for inclusion in the 'social information' and 'non-seeded' groups were all given a further ten hours of opportunity for solution and open diffusion with the inefficient method partially blocked in this way. Following Yamamoto et al. (2013), if individuals in the 'social information' groups failed to switch, they were provided with salient human demonstrations of the efficient method by SJD after this second period of open diffusion, because our question is not about chimpanzees offering such models, but rather how chimpanzees respond to such models when available. The 'naïve' group was not included in Experiment 2 as not only were they already exclusively using the efficient method of extraction, but their initial inclusion was designed primarily to investigate how solution naïve chimpanzees would approach this problem.

3.1 EXPERIMENT 2: METHODS

Methods followed those outlined in the Testing phase of Experiment 1 Methods with the exception that the token was now placed in an indent in the floor located directly behind (from the chimpanzee's perspective) extraction point B (Fig.1). This impeded movement of the token along the length of the apparatus. The 'naïve' group was not included in Experiment 2. Following Yamamoto et al. (2003), if individuals within the 'social information' groups failed to switch, they were provided with salient demonstrations of the efficient method by SJD after this second period of open diffusion (one individual did not receive human demonstrations as she did not wish to separate from her group). To avoid unnecessary voluntary separation of participants from their group, so long as a participant was able to gain access to the Serialbox, human demonstrations were given in the presence of other group members. If instead the participant struggled to gain access, they were offered the opportunity to voluntarily separate and given additional demonstrations over a period lasting no more than 30 minutes. After the participant attempted the inefficient method, SJD pulled the apparatus back and demonstrated use of the door. If

participants were still attempting to use the inefficient method, SJD provisioned the apparatus with the door already open, facilitating extraction via point B.

3.2 EXPERIMENT 2: RESULTS

Extractions within the test period

In the 'social information' groups, the chimpanzee models demonstrated a 100% success rate of token extraction via the efficient method; in contrast, use of the inefficient method had a median success rate of only 25% (range 0 – 93%) (Appendix 4 Tables S1 and S2: a failed attempt was one in which a participant manipulated the Serialbox but subsequently left the apparatus without successfully extracting the token). Success rate became significantly lower in Experiment 2 (E2) compared to Experiment 1 when using the inefficient method (One-tailed Wilcoxon Signed ranks test Z = -2.84, n = 10, P = 0.001, $median_{E1}$ = 100%, $median_{E2}$ = 25%, r = -.64). If participants were successful in extracting the token via the inefficient method, latency to extraction was almost two and a half times longer than a successful extraction in Experiment 1 (E1 median = 33.6 seconds, range = 24.5–51.8; E2 median = 83 seconds, range 66.1–556; See Appendix 4 Table S2 for comparisons with models' efficiency).

In the 'non-seeded' groups, one individual now discovered and used the easier efficient method (Individual *Kt*), and was witnessed by two other individuals, *Na* and *Ae*. These two did not then acquire the method; however, they had observed *Kt* only three and two times respectively. No other individual was observed to use the efficient method in the 'non-seeded' groups, with success rate dropping for all other participants (median success rate of 14.3%, range 0 – 50%). Success rate was significantly lower in E2 than in E1 for those using the inefficient method in the 'non-seeded' groups (One-tailed Wilcoxon Signed ranks test Z = -2.38, n =7, P = 0.008, $median_{E1}$ = 100%, $median_{E2}$ = 14.3%, r = -.64). Success rate for those using the inefficient method did not differ between the 'social information' and 'non-seeded' groups (Mann Whitney U = 28, n = 17, P = .494).

Switching behaviours

To assess switching behaviours in the 'social information' groups, the percentage of efficient extractions [efficient extractions/(efficient extractions + inefficient extractions) x 100] observed throughout E2 for each participant was compared with the percentage of efficient extractions observed during E0, using a one-tailed Wilcoxon signed rank test. There was now a significant switch, with five individuals in the 'social information' groups switching from the

inefficient method to using the more efficient method that continued to be demonstrated by the model [Z = -2.023, n = 11, P = 0.031, median$_{E0}$ = 0% (mean = 0 %), median$_{E2}$ = 0% (mean = 36.1%), r = -.43; Fig. 2].

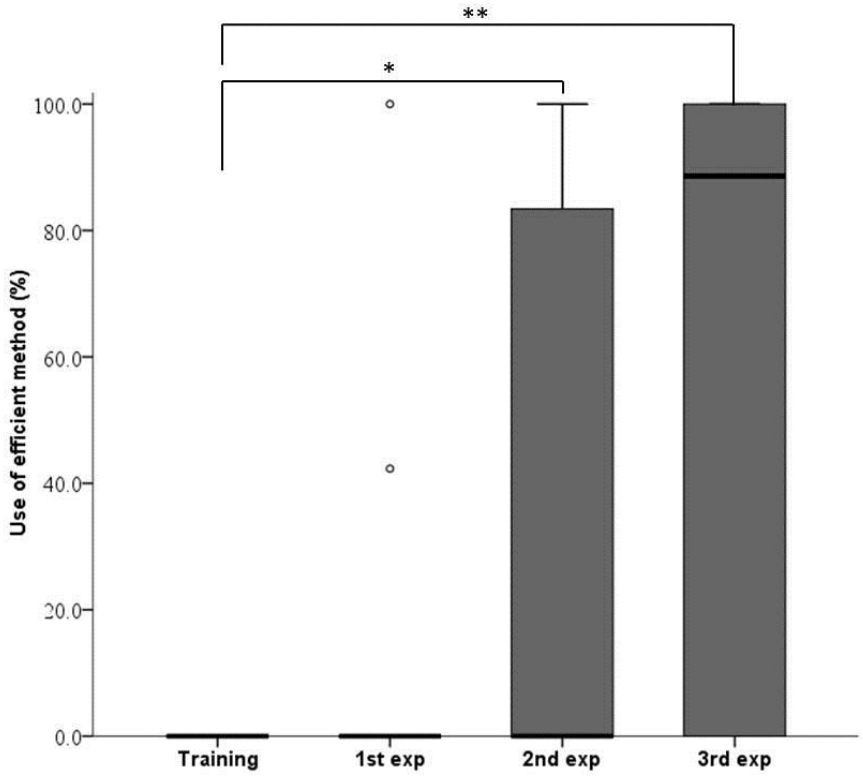


Figure 2. Percentage use of efficient method in Training and Experiments 1, 2 and 3 for individuals in the 'social information' groups. The line represents the median, the bottom and top of each box indicate the 25th and 75th percentile respectively, the whiskers show the minimum and the maximum values that are not considered outliers (i.e. values > 1.5 times the interquartile range from the 25th or 75th percentile), outliers are represented by circle with values over three times the 75th percentile value. * indicates a P value of less than 0.05 and ** less than 0.01.

Human demonstrations

After additional human demonstrations (median demonstrations given = 12, range = 10-17), four additional participants from the remaining six switched to using the efficient method in the 'social information' groups.

Use of efficient method in 'social information' and 'non-seeded' groups:

To determine the role of social information in behavioural upgrading, a one-tailed Fisher's exact test (applied due to expected values less than 5) compared the frequency of chimpanzees using the alternative method between those in 'non-seeded' groups and the 'social information' groups. A significant association was found between exposure to sustained social information and whether or not individuals switched to using the efficient alternative (P = 0.005) (Fig. 3). Based on the odds ratio, the odds of switching were 31.5 times higher for those in the 'social information' groups than those in the 'non-seeded' groups. As noted above, the two individuals who observed *Kt* in the 'non-seeded' group performing the efficient method did not acquire it, but they observed only three and two times respectively, whereas those in the 'social-information' groups had a median of 31 observations before acquisition (range 15-169); Appendix 4 Table S3).

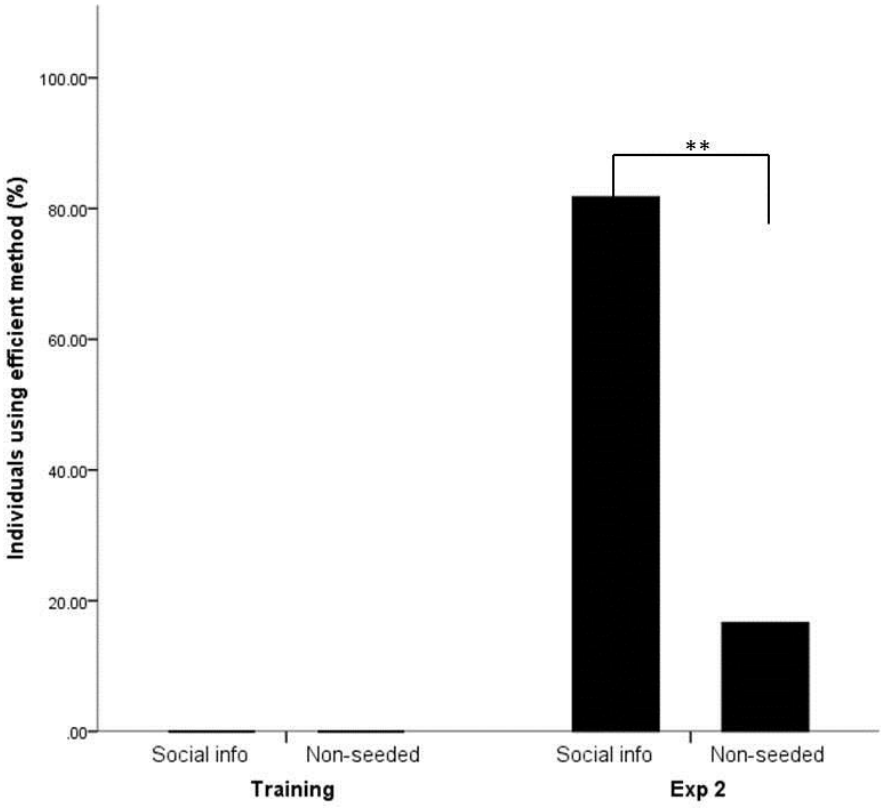


Figure 3. Percentage of individuals within the 'social information' groups and' non-seeded' groups who used the efficient method across training and Experiment 2. ** indicates a P value of less than 0.01

3.3 EXPERIMENT 2: DISCUSSION

In all, nine of the 11 chimpanzees in the 'social information' groups were eventually able to flexibly change their behaviours by relinquishing their mastered technique and switching to a novel one. We infer that this was due to the greater contrast between participants', inefficient use of extraction at point A and the more efficient use of extraction at point B displayed by the model, a contrast that involved differences in both latency to extraction and proportion of successful extractions.

An alternative possibility, that the changes occurred because of the extended time frame of adding E2 to E1, affording more observations of the model, can be rejected for several reasons. First, E1 involved a long period in which any switching at all was rare, and moreover, participants not switching in E1 persevered with their inefficient technique despite both multiple observations of the model (median 19 observations, range 11-57) and multiple token extractions using their inefficient method (median 18 attempts, range 4-119 among those that switched in Experiment 2). In addition, among chimpanzees who did switch at some point, the number of observations of the model did not predict the number of manipulations they would take before switching (final two columns in Appendix 4 Table S3). Given these considerations and that (i) only two participants were seen to open the door at point B in E1, and critically, (ii) no other individual was observed to make any persistent attempts to open the door until their behaviours became highly inefficient in E2, we conclude that the switch in behavioural strategy in E2 can be ascribed to the change in the relative efficiency of the options that were experimentally engineered between E1 and E2.

Five of the switching chimpanzees showed relatively low levels of behavioural conservatism, with two having previously upgraded their behaviours in E1, the other three adopting the alternative once their own approach became highly inefficient in E2. This was clearly facilitated by social information, as demonstrated by a lack of switching (bar one individual) in the 'non-seeded' groups. The social learning involved may have relied on only relatively simple processes such as stimulus enhancement (of token extraction at point B) or more complex ones, like emulation or imitation, and our study was not designed to discriminate among these. In any case, stimulus enhancement or any other social learning was insufficient for change despite extensive exposure in Experiment 1; it had effects only when the contrast in efficiency became more extreme.

Other chimpanzees still displayed a high degree of behavioural conservatism, in line with previous research (Bonnie et al., 2012; Dean et al., 2012; Hopper et al., 2011; Hrubesch et al.,

2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009), showing a difficulty in inhibiting use of a highly inefficient established behaviour, with varying levels of perseveration. This was most evident in the 'social information' groups, where despite many observations of a far more efficient alternative, six individuals continued in their old behaviour for some time, with four only switching behaviours following salient social information engineered though human demonstrations, and the two remaining individuals never relinquishing their inefficient solutions.

There was also very little exploratory behaviour in the 'non-seeded' groups, with only one individual discovering the efficient method. Despite witnessing the efficient solution, two individuals within the 'non-seeded' groups never attempted this alternative method. This was most likely due to their more limited and inconsistent exposure to demonstrations of this method, and highlights again the conservative nature of chimpanzee behaviour. Although there was no direct relationship between the number of observations of the model and number of manipulations taken before switching, no individual within the 'social-information' groups was seen to switch after as few demonstrations as experienced by these 'non-seeded' individuals, indicating the potential need for relatively sustained social information across repeated attempts to solve the Serialbox. This mirrors findings in humans whereby trial and error learning interacts with repeated exposure to socially available alternatives to produce behavioural change (Wiley, 1998).

Whilst these results show some degree of behavioural flexibility, it remained to be seen whether chimpanzees could express such flexibility in a cumulative fashion; that is, could chimpanzees "add an existing technique used in a different context, or an entirely novel technique, to an existing technique, and integrate them functionally" (Pradhan, Tennie, & van Schaik, 2012, pg 181): could they now integrate the efficient method they had acquired (door pull and extraction at point B) with behavioural elements common to the inefficient method (lid lifting and hole poking) to cumulatively produce the efficient solution demanded by the scenario used in Experiment 1? In Experiment 1 only two chimpanzees were observed to do this, with the majority instead sticking to their known behaviours despite potential gains in extraction efficiency. Now however, seven additional chimpanzees within the 'social information' groups and one from the 'non-seeded' groups had mastered use of an alternative, independent solution (door pull and extraction at point B), which could potentially be combined with other known behaviours (elements of the inefficient solution) to produce a compound technique that they were previously not seen to use when some of these elements were novel.

4. EXPERIMENT 3: MODIFYING, INHIBITING AND BUILDING ON EXISTING BEHAVIOURS

To investigate chimpanzees' potential for such accumulation, the token was repositioned in the same location as in Experiment 1 (i.e. it was removed from the indent in the floor so its movement was no longer impeded), and could now be successfully extracted at either point A using the methods of E0, or from point B (Fig. 1). To extract from point B, individuals had to employ initial elements from their learned, inefficient technique (lid lifting and hole poking) but inhibit the remainder of the sequence resulting in extraction at point A and instead combine lid lifting and poking with the element unique to efficient extraction (the door pull at point B). Alternatively, individuals could now revert back to using their earlier well-practiced inefficient technique, with this method reliably yielding the token, but much more slowly.

4.1 EXPERIMENT 3: METHODS

The token was again placed inside the apparatus three quarters of the way along the first compartment (as in Experiment 1). The apparatus was presented over five hours to all participating chimpanzees (19 individuals across the 'social information' and 'non-seeded' control groups), with both the efficient and inefficient methods as viable strategies to extract the token, following the procedure outlined in the Testing phase of Experiment 1 Methods.

4.2 EXPERIMENT 3: RESULTS

Extractions within the test period

One individual in the 'social information' groups and three individuals in the 'non-seeded' groups chose not to participate during the test period ('E3' –Appendix 4 Table S1).

Switching behaviours

In the 'social information' groups, there was a significant change of behaviour from use of the earlier, trained inefficient method, with seven individuals now using the more efficient compound solution needed (One-tailed Wilcoxon signed rank test comparing percentage use of efficient behaviours: $Z = -2.410$, $n = 10$, P = .008, $\text{median}_{E0} = 0\%$, $\text{median}_{E3} = 88.2\%$, $r = -.54$; Fig, 2). In the 'non-seeded' groups, one individual, *Kt,* also built on her prior solution to use the more efficient method. No additional individuals in the 'non-seeded' group used the efficient method of extraction, with four exclusively sticking with the inefficient solution.

At the individual level, of those with personal experience of the efficient method (n = 9 'social information' participants and n = 1 'non-seeded' participant), seven showed a significant change of behaviour from their initial inefficient method to using the efficient compound solution (one-tailed Fisher exact tests with Bonferroni corrected P value = 0.005), whilst three reverted back to preferentially using the inefficient method (P > 0.005). In sum, five exclusively used the efficient method, three flexibly switched between using both methods, and two exclusively returned to the inefficient method (Fig. 4; Table 2).

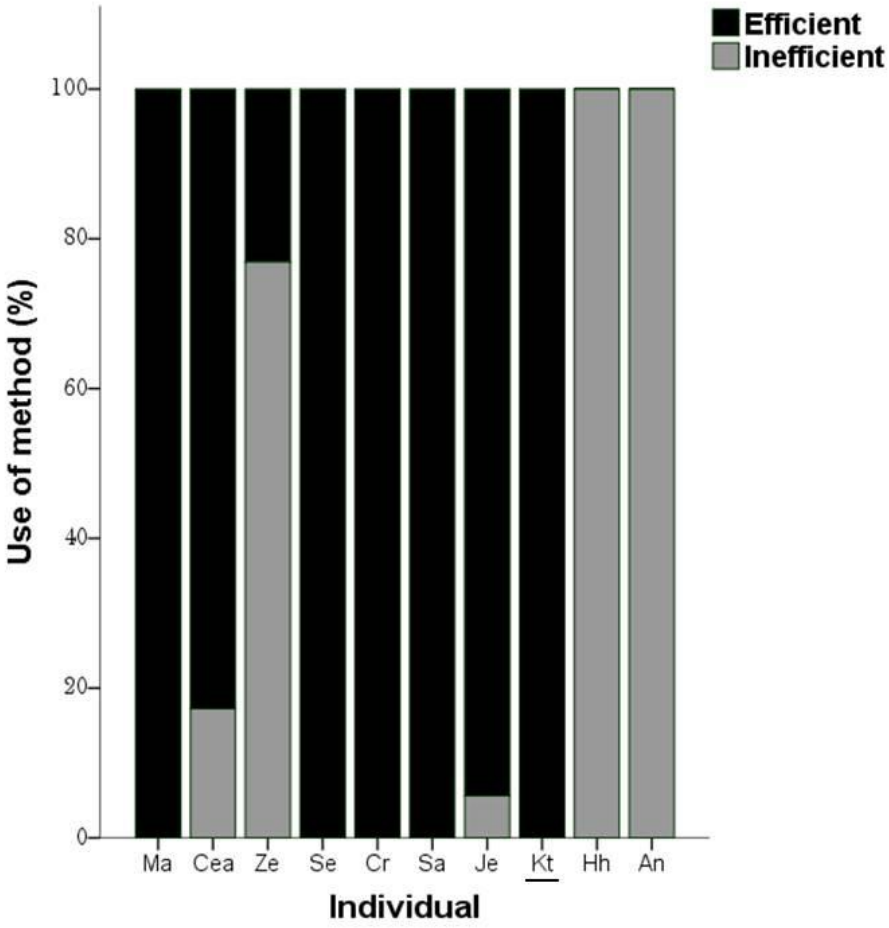


Figure 4. Percentage use of the inefficient and efficient solution of token extraction in Experiment 3 for each individual with prior experience of extraction via point B during Experiment 2. The 'non-seeded' individual *Kt* is underlined, with all other individuals being 'social-information' participants.

Table 2.
Summary of participant's behaviour in the 'social information' groups as well as the innovator (*Kt*) in the 'non-seeded' group.

	Exp 1	Exp 2		Exp 3
Individual	Old solution somewhat inefficient	Old solution highly inefficient	Human Demos	Old solution somewhat inefficient
Sa	Build	Switch	N/A	Build
Se	Build/revert	Switch	N/A	Build
Ma	Stay	Switch	N/A	Build
Cea	Stay	Switch	N/A	Build
Ze	Stay	Switch	N/A	Build
Kt	Stay	Switch	N/A	Build
Cr	Stay	Stay	Switch	Build
Je	Stay	Stay	Switch	Build
Hh	Stay	Stay	Switch	Revert
An	Stay	Stay	Switch	Revert
Ta	Stay	Stay	N/A	Stay
Si	Stay	Stay	Stay	N/A

'Build' denotes building on the inefficient solution. 'Stay' denotes maintaining use of the inefficient solution. 'Revert' denotes reverting back to the inefficient solution after having efficiently extracted through point B. 'Switch' denotes relinquishing the inefficient solution in favour of using the door and extraction at point B. 'N/A' represents no participation in this phase. The non-seeded innovator (*Kt*) is highlighted in grey.

4.3 EXPERIMENT 3: DISCUSSION

Seven chimpanzees in the 'social information' groups now displayed the efficient solution employed by the models. Only two of these individuals had previously been seen to use this efficient solution, when this required the addition of a novel element, in E1. The other five, along with the innovator *Kt* in the non-seeded' group, displayed a cumulatively built combination of elements they had learned in E0 and E2. From the results of E3 we conclude that accumulation involved the combination of behaviour routines already in the repertoire. One of these, opening the door at point B (even if it was the case that this was acquired only by affordance learning about the significance of this door, but also if it involved copying the action sequence involved),

gave rise to behavioural routines that could be combined with parts of an earlier-acquired procedure, of opening lids and poking, learned via training in E0. Chimpanzees' successes in E3 additionally displayed an ability to flexibly inhibit the remainder of the trained routine for extraction at point A. Such capacities for cumulative combination, although modest compared to full cumulative culture, could, we submit, provide important foundations for cumulative culture if present in ancestral states.

5. GENERAL DISCUSSION

Chimpanzees were trained to use a relatively laborious sequence of actions to extract a valuable food-token from a puzzle-box. This initial method was sufficiently complex to require socially-facilitated acquisition in most chimpanzees and we ensured it was then extensively practiced, to become routine, as in cultural behaviours in the wild. A different, more efficient alternative was then demonstrated by a high ranking female conspecific. This new solution involved partial use of behaviours in common with the established extraction technique as well as the addition of a novel element.

When chimpanzees could still successfully forage with their established method (in E1), only a small minority relinquished this and flexibly upgraded to the more efficient alternative witnessed. The predominant failure to switch to the more efficient technique is consistent with earlier reports of chimpanzee conservatism (Bonnie et al., 2012; Dean et al., 2012; Hopper et al., 2011; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Price et al., 2009) and may offer a partial explanation for the relative stasis of chimpanzee culture. However, when their established behaviours were made considerably more inefficient in E2, most chimpanzees observing a knowledgeable individual were able to relinquish their inefficient behaviour and flexibly switch to using an alternative strategy. When in E3 they were again challenged by the task configuration of E1, the majority of these chimpanzees showed an ability to build on prior behaviours by combining already acquired elements of their learned use of the door for extraction at point B and parts of their earlier technique for extraction at point A. They had not achieved this earlier in E1, when success required the addition of a *novel* behaviour to the sequence. The cumulative combinations recorded in E3 thus stand in contrast to the findings of previous studies where chimpanzees appear behaviourally inflexible (Dean et al., 2012; Marshall-Pescini & Whiten, 2008). Our results suggest that in certain contexts at least, chimpanzees may combine *known* behaviours to match an efficient compound technique demonstrated by others.

Although chimpanzees show a considerable degree of behavioural conservatism, we suggest these results indicate that they also have an ability to combine independent behaviours to produce more efficient compound action sequences. Such an ability, while not yet truly cumulative, may be one of the foundational abilities (or candidate mechanisms) for human cumulative culture, through the ability to "add an existing technique used in a different context ....to an existing technique, and integrate them functionally" (Pradhan et al., 2012, pg 181). This shares similarities with human studies in which recombination of behavioural variants is employed to move solutions closer to an optimum (Boyd, Richerson, & Henrich, 2011; Derex, Feron, Godelle, & Raymond, 2015; Enquist, Ghirlanda, & Eriksson, 2011; Kempe & Mesoudi, 2014; Muthukrishna, Shulman, Vasilescu, & Henrich, 2014; Youn, Strumsky, Luis, Bettencourt & Lobo, 2015) that is, accumulation may commonly be brought about through novel recombination of existing behaviours creating "innovations without invention, creativity or trial and error learning" (Muthukrishna et al., 2014, pg 5).

Whilst we offer evidence for a potential core prerequisite of cumulative culture, this is not evidence of cumulative culture itself, as the behaviours of interest were also produced spontaneously by one chimpanzee we studied, and they do not require the combination of multi-generational contributions by several innovators, which is inherent to full-blown cumulative culture (Tennie, Call, & Tomasello, 2009). Further, our study was not designed to dissect exactly how the chimpanzees were learning from the available social information, whereas advanced cultural accumulation is thought to depend on high fidelity transmission (Lewis & Laland, 2012), as well as cognitively complex learning heuristics (Laland, 2004; Tomasello, Carpenter & Hobson 2005). However, chimpanzees in our study were able to use multiple solutions as well as to build on and combine prior behaviours to efficiently solve an extractive foraging problem, indicating greater potential for cumulative change than found in many earlier studies and emphasized in recent reviews (e.g. Henrich, 2015). The accumulation observed here lends support to the plausibility that some behaviour exhibited by wild chimpanzees is actually the result of a cumulative process, even if elementary compared to that observed in human culture (Boesch, 2003; Boesch, Head, & Robbins, 2009; Humle, Snowdon, & Matsuzawa, 2009; Sanz, Call, & Morgan, 2009; Sanz, Schöning, & Morgan, 2010).

CHAPTER 7: DISCUSSION

Hypothesis 1: behavioural optimisation (use of Solution B) is hindered by having knowledge of an alternative solution (A) i.e. behavioural inflexibility limits cultural evolution

Hypothesis 2: behavioural optimisation (use of Solution B) is hindered by some other factor that prevents learning of solution B, but not Solution A i.e. another factor limits cultural evolution

1. SUMMARY OF FINDINGS

Taken together, my results suggest that chimpanzees' conservatism is in part caused by complexities in the behaviours concerned, both when relinquishing such behaviours, or adding such behaviours to established ones, and this may be constrained by cognitive resource availability. Chapter 4: A not B and Chapter 5: Biways & Pitfall, largely support a Hypothesis 1 interpretation of suboptimal behaviour, with evidence for both Hypothesis 1 and 2 apparent in Chapter 6: Serialbox. I suggest that these findings are particularly relevant for cumulative culture, and may partially explain the relative stasis of chimpanzee compared to human culture.

In Chapter 5: Biways, I found chimpanzees had little difficulty relinquishing prepotent, simple behaviour (Solution A) in favour of a simple, more optimal alternative (Solution B). This is consistent with some prior research (Hopper, Kurtycz, Ross, & Bonnie, 2015; Van Leeuwen, Cronin, Schütte, Call, & Haun, 2013; Yamamoto, Humle, & Tanaka, 2013). Building on some of these previous studies, I included controls to find a clear effect of social information and payoff on the likelihood of adopting Solution B. Indeed, the extent of behavioural flexibility exhibited by these chimpanzees exceeds that of previously tested chimpanzees in a social setting; for example, van Leeuwen et al. (2013) found only three of the six chimpanzees modified simple behaviour in the presence of social information to adopt a more productive and simple Solution B, whereas in Chapter 5: Biways, all chimpanzees did. This may be due to methodological differences: van Leeuwen et al. used a token task, which involves some level of abstraction for participants. There were also quite a few instances of reversions whereby having sampled solution B, participants reverted to solution A. This may indicate a poor understanding of the task contingencies. In contrast, there were very few reversions to Solution A in the comparable Biways study.

In Chapter 5: Pitfall Study 2.1 & Chapter 6: Serialbox Experiment 3, similar to Manrique et al. (2013), I found chimpanzees would readily build upon behaviours when all elements of accumulation were within their repertoire. However, Solution A in these cases may be

considered more prepotent and complex than those in Manrique et al., requiring long periods of learning before mastery. In contrast, when building upon complex behaviours required the partial inhibition of Solution A, chimpanzees showed behavioural conservatism, perseverating with a suboptimal response in favour of a superior alternative (Serialbox Experiment 1 and Pitfall Study 2.2 (cf Hrubesch et al. 2009). This was especially apparent when accumulation involved incorporating a novel/complex element (Serialbox Experiment 1). Similarities between Serialbox Experiment 3 and Marshall-Pescini and Whiten (2008) exist in that both involved a prepotent, complex solution A and a complex B solution, and both saw high levels of preservative behaviour; however, it is unclear if inhibition of Solution A was required to use Solution B in Marshall-Pescini and Whiten.

Finally, Chapter 4: A not B sits as something of the odd one out, in that it is a purer measure of executive function, and not necessarily representative of the myriad of cognitive processes that affect decision-making in real-world situations. It followed to me that if chimpanzees do have reduced inhibitory control, we might expect to see this in the A not B paradigm; however, it would have also been possible to find chimpanzees performed well on this task, as children over one year of age do not tend to commit perseverative errors in A not B despite making errors on more complex tasks (e.g. Zelazo 2006). That being said, if children experienced the same level of A trials as chimpanzees in Chapter 6, we might expect to see greater perseverative errors than on the traditional three A followed by one B trial format (Marcovitch & Zelazo, 2009). It is important to note that I did not continue to test chimpanzees on the B trial to investigate for how long they would perseverate with solution A. It would be my estimation that they would have rectified their solution choices within a few trials, and, like the Biways study, not shown high levels of conservatism. Overall, Chapter 4 signals that inhibitory control is compromised in chimpanzees, and lends support to a Hypothesis 1 interpretation of suboptimal behaviour; that is, solution A directly impacts upon adopting Solution B

Executive function and inhibition are central themes throughout all chapters, and while I comment on how cognitive load likely taxes working memory, and detracts from resources required for inhibition, I do not directly say how. It is possible that increasing the load on working memory detracts from the ability to amplify relevant information within working memory, or alternatively, leaves less cognitive resources to suppress irrelevant information. I do not attempt to disentangle the nature of inhibition with the work I have presented in this thesis; however, in the next section, I will attempt to draw together different threads of research to speculate as to how cognitive load is related to cognitive control, habit formation, social learning and decision-

making heuristics. These are all important and interrelated factors affecting the optimisation of behaviour. Given that cumulative culture is usually associated with gains in productivity or efficiency, factors which affect behavioural optimisation are thus highly relevant to cumulative culture, if not the same.

2. CAUSES OF SUBOPTIMAL BEHAVIOUR

2.1 EXPLORE VERSUS EXPLOIT DECISIONS HEURISTICS

A key component of behavioural change lies in the heuristics guiding when to stop exploiting a known solution and begin exploration for a new, potentially better one (Cohen, McClure, & Yu, 2007; Daw, O'Doherty, Dayan, Dolan, & Seymour, 2006; Montague, King-Casas, & Cohen, 2006; Holmes and Cohen, 2014). When an individual already has a working solution, they may be less likely to adopt alternatives (Strimling, Enquist, & Eriksson, 2009; see also Rendell et al., 2010). This may be because the current exploitative outcome of a known solution is more attractive than the investment of resources (both cognitive and energetic) in exploring alternatives (Holmes and Cohen 2014), which although potentially more beneficial in the long term, may also involve a period of trial and error learning during which there is no return (Rushworth, Kolling, Sallet, & Mars, 2012).

This would be especially pertinent when alternative behaviours are complex, and so require a relatively long period of learning before mastery (Fang & Levinthal, 2009). Such costs of exploration may be offset by capitalising on social information (Montague et al., 2006; Toelch, Bruce, Meeus, & Reader, 2011) with more complex behaviours often adopted through socially facilitated acquisition (Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009); indeed, human culture may be transmitted through mechanisms which reduce the costs of exploration by allowing high-fidelity copying, perhaps even without insight into the underlying mechanics of the behaviour (Csibra & Gergely, 2011; Horner & Whiten, 2005). Interestingly, research also suggests that a potential driving force behind hominin cumulative culture is the recombination of behavioural variants (Boyd, Richerson, & Henrich, 2011; Derex, Feron, Godelle, & Raymond, 2015; Enquist, Ghirlanda, & Eriksson, 2011; Kempe & Mesoudi, 2014), creating "innovations without invention, creativity or trial and error learning" (Muthukrishna, Shulman, Vasilescu, & Henrich, 2014, pg.5), which may be considered another low risk form of exploration (Youn, Strumsky, Luis, Bettencourt & Lobo, 2015).

Additionally, research which focuses on learning heuristics and the trade-off between exploration and exploitation suggest a role for social learning in decision algorithms guiding

behaviour optimisation, with individuals incorporating an evaluation of their own behaviour's outcome to that of observable others (Burke, Tobler, Baddeley, & Schultz, 2010; Montague et al., 2006). Such accounts help explain why social learning can facilitate the optimisation of behaviours (Rendell et al., 2010). One key social learning heuristic potentially underlying cumulative culture is a copy-when-better strategy (Laland, 2004; Mesoudi, 2011b). It has been suggested that animals may not be able to evaluate relative payoffs between their own actions and those of others, by, for example, employing 'copy-when-dissatisfied' strategies as opposed to a 'copy-when-better' rule (Laland, 2004; Schlag, 1998). This may in turn hinder behavioural optimisation and accumulation (Marshall-Pescini & Whiten 2008). Chapter 5: Biways Study 1.1 presents strong evidence of such an ability; that is, socially facilitated modification of behaviour for an increased payoff (also see Hopper et al., 2015; van Leeuwen & Call, 2016; van Leeuwen et al., 2013). Another key consideration is how social information is used. In Chapter 5: Biways and Pitfall, I suggested that individuals capitalised on the social information available, and because behavioural modification in these studies were already well within the repertoires of the participants, social information likely facilitated optimisation by providing insight into the affordances of the apparatus. What is also possible, beyond how information is extracted from observation, is that social information in and of itself encourages exploratory behaviours. By this I mean the cost of exploration is mitigated by witnessing another individual successfully using this alternative behaviour for, for example, a greater payoff, as this may not only yield some information about the affordances or processes involved, but also indicates there exists another solution which may be better than a currently held one (Toelch et al., 2011), Interestingly, Nedic et al. (2012) found human adults were able to optimise their behaviours using social information regarding the behavioural choices of others. However, when presented with only the results of these others' choices (not the behavioural pathways to obtaining those results), this alone encouraged exploratory behaviour. This is perhaps because seeing these outcomes indicated that a more optimal behaviour existed than the participant's own current one. Importantly, this unguided exploration was sometimes deleterious, with an overall reduction in final reward accrued. This highlights an important caveat of social information: In general, when behaviours are simple, and therefore easy to master, there is less cost to exploring alternatives as the individual will not have to engage in extensive trial and error learning. However, when behaviours are complex, and not easily converged upon, an inability to parse process information from social information may result in costly exploration, with a decrease in behavioural optimality. As such, an ability to engage in high-fidelity copying could be quite an important factor underlying cost

reduction when exploring alternative behaviours, and has been highlighted may times, likely one of the reasons humans have cumulative culture (Tennie, Call, & Tomasello, 2009)

2.2 EXPLORE VERSUS EXPLOIT AND EXECUTIVE FUNCTIONS

I believe the Serialbox provides some insights into how chimpanzees optimise behaviour when both solution A and B are complex, encompassing support for both Hypothesis 1 and 2, and highlights the multi-faceted nature of behavioural change when examining behaviours which better approximate cumulative culture. From Serialbox Experiment 1, when chimpanzees could still successfully forage with their established method, only a small minority relinquished their old solution and flexibly upgraded to a more efficient alternative. Although two out of five naïve controls were able to perform Solution B, it took them around two hours before doing so. Three other individuals failed to solve either Serialbox Solution A or B despite interacting with the box. This is in contrast to Biways and Pitfall where Solution B was converged on much earlier, and by all participating chimpanzees. This makes it more difficult to conclude definitively that having a prior solution in and of itself hindered behavioural optimisation within the Serialbox task. Instead, alternative explanations (Hypothesis 2) may also explain suboptimal behaviour. When individuals had a working solution (Experiment 1) the majority did not use social information or exploratory behaviour to upgrade to a more efficient behaviour. We might consider that under certain circumstances, and as outlined above, when a known solution is still functional, chimpanzees may not be willing to invest in learning a new one. Specifically, within the Serialbox task, high levels of response prepotency and the complexity of solutions, may have militated against behavioural change, as whilst behaviourally the alternative method is more efficient, cognitively, it may be quite costly to relinquish an old solution through inhibition, and learn a new solution through what may be a lengthy trial and error process (Holmes & Cohen, 2014). Additionally, the benefit of this may have been minimal, with gains in response efficiency not motivating investment. As we found no effect of social information on behaviour in Experiment 1, we should also consider that having a working solution may decrease attending to relevant external cues; this is somewhat reminiscent of a 'copy-when dissatisfied' social learning strategy, whereby an individual is most attuned to social information when their personal strategy is unsatisfying (Laland, 2004; Marshall-Pescini & Whiten, 2008; Yamamoto et al., 2013 see also Braet et al., 2009; Hester et al., 2009 for related arguments relating to attention and behavioural inhibition in humans). However, given we found an effect of social information in both Biways and Pitfall, when chimpanzees also had working solutions, we should be cautious in that interpretation.

In Serialbox Experiment 2, by partially blocking the initial solution, we altered the nature of both solution A and B: The decreased reliability of established behaviour A perhaps reduced response prepotency. Although participants perseverated quite strongly with this now extremely inefficient response, with only a 25% success rate, it is highly likely that over time, response prepotency decreased due to repeated failure. The repositioning of the token meant that participants no longer had to build on Solution A to achieve Solution B. This may have simplified Solution B somewhat, although the action of pulling open the door still remained novel to participants. Again, in line with human studies, given the extensive practice chimpanzees had with their original inefficient solution, and the cognitive load of behaviours, it is perhaps expected that we see high levels of behavioural conservatism with emerging behavioural flexibility: with time, new solutions may be converged upon due to a combination of exposure to alternative solutions as well as the weakening of response prepotency (Wiley, 1998); that is, behaviour resulting from the combination of personal experience with social information (Derex et al., 2015; Mesoudi, 2011a; Rieucau & Giraldeau, 2011; Whalen, Cownden, & Laland, 2015). This style of learning has been suggested to underlie not only the acquisition of complex behaviours in wild chimpanzees but also technologies in our hominin line (Whiten, 2015). It is not possible to quantify exactly how social information was incorporated into the behaviour of the chimpanzees in Experiment 2, as this would be likely confounded with social information in Experiment 1; that is, we cannot say for certain that chimpanzees did not acquire knowledge about Solution B in Experiment 1. However, interestingly, studies with humans indicate a role for increased attentional control after failures on tasks (Braet et al., 2009; Hester, Madeley, Murphy, & Mattingley, 2009).

This highlights an important consideration of how social information is used. The open diffusion methodology in Chapters 5 and 6 is such that continued use of Solution A by participants in our experimental groups (IPSI in Biways and Pitfall, social information groups in Serialbox), will positively correlate with the number of observations of Solution B by the model: both increase as a function of time. To avoid confusion within analyses, I coded social information in a binary fashion: you either have it or you do not. However, to paraphrase a reviewer who critiqued the Serialbox study during the publication process, it could be that chimpanzees reached what may be considered a 'threshold of information' which then resulted in behavioural change. This is a possibility, and additionally, it may also be that with time, we should expect some spurious exploration. However, I would argue that the variability we see in chimpanzee perseveration across tasks, not only in my own work but in that reviewed in Chapter

2, may complicate this picture; for example, Marshall-Pescini and Whiten (2008) found most chimpanzees did not adopt Solution B despite witnessing over 180 demonstrations. To examine if results could be explained by some information threshold, I compared the number of solutions taken to converge on solution B between Biways and Pitfall study 2.1, where no or relatively minimal perseveration was seen, with solutions taken in Pitfall Study 2.2, where evidence of perseveration were found (note that this topic has already been specifically addressed for the Serialbox in Chapter 6). If behavioural change is underlain by reaching some threshold of information, we should expect to see adoption of Solution B at similar rates across these studies, and that perseveration is a result of not having reached that critical threshold. Analyses show this is not the case, with individuals within Biways and Pitfall Study 2.1 (no effect of prior solution) adopting solution B after an average of 26 (range 3-54) and 7 (1-18) witnessed solutions respectively. In contrast, those in Pitfall study 2.2 (effect of prior solution) witnessed Solution B 10 (range 1-20) times before adopting it. Naïve individuals converged on solution B in both the Biways and Pitfall 2.2 studies after 4 (range 0 – 14) and 5 (range 0-10) social observations respectively. This indicates that social information as measured on a continuous scale does not easily explain the pattern of perseveration seen, and ultimately, very little information was needed about Solution B to adopt it. In general though, the methodology I have used does not lend itself to this form of analysis: a dominant female always modelled Solution B, with lower ranking chimpanzees having to wait until she moved away from the apparatus before they could participate. Typically this resulted in a high number of observations of the model, with relatively fewer opportunities to personally interact with the task. Overall however, data is most consistent with perseveration being linked to the complexity of solutions.

I believe the picture changes when we consider behaviour where solution complexity precludes either complete innovation by a single individual (as in true cumulative culture), or behaviours which are only within the capabilities of a rare innovator (Whiten et al., 2009). Here we might expect an interaction effect between having a prior solution and exposure to social information considered on a continuous scale (as opposed to the binary analyses I employ). As highlighted in Chapter 1, when attempting to learn a complex behaviour, there are likely to be repeated learning attempts, which should incorporate both social and trial and error learning (e.g. Whiten, 2015). Therefore, when looking at behavioural flexibility which involves a complex Solution A and a complex Solution B, it is hard to disentangle the effects of social information from the effects of prior solution on adoption of Solution B, as here social information may be needed for acquisition (as opposed to only facilitating it as in both Biways and Pitfall). Further,

other considerations that I've highlighted above need to be minded, such as how likely an agent is to invest resources in learning a complex behaviour, especially if they already have a working solution, and how that will be affected by the way in which information is extracted from observations (i.e. is process information necessary). This suggests we need to consider explanations that incorporate both Hypotheses 1 and 2.

Returning to the Serialbox, Experiment 3 mirrors Pitfall Study 2.1, where chimpanzees were tasked with combining known behaviours (or those well within their innovative capabilities) to optimise outcome. In both these studies, chimpanzees readily built on behaviours, indicating that chimpanzees have little problem with accumulation when composite elements are known to them (cf Manrique et al., 2013). Interestingly though, note that in both these conditions, chimpanzees were not necessarily having to inhibit a prepotent response. This is in contrast to both Serialbox Experiment 1 and Pitfall study 2.2, where inhibition of a well-practiced complex action sequence is required, and where perseveration was evident. Further, both Serialbox Experiment 1 and Pitfall 2.2 not only involve a higher level of complexity than Biways (where inhibition was also required) but they also differ on another feature; the optimum behaviour (Solution B) involves only a partial inhibition of Solution A, and incorporates components of A (*lift lid* in Serialbox and *slide box* in Pitfall). This is reminiscent of some technological accumulation, whereby, for example, the construction process is interrupted at some mid-point and modified, as opposed to building onto the end or fully relinquishing the variant. It may be that using elements of Solution A primes the full expression of A, making inhibition at some intermediate point more difficult than if no elements of Solution A had been employed (Houghton & Tipper, 1994). For example, Cragg and Nation (2008) found on closer inspection of a Go/No-go task that a substantial amount of inhibitions involved first initiating the response and then successfully terminating it before completion, with older children (9-11 years versus 5-7 years) being better at this i.e. successful inhibition may not be necessarily characterised by totally relinquishing a response, but rather, an ability to terminate a response part way through, and this may be dependent on cognitive resources (as evidence by the effect of age). Interestingly, this draws parallels with research in habit formation, where evidence suggests that in chunked behaviours, execution of the initial element of the chunked sequence is a powerful predictor of whether or not the full habitual response is expressed (Smith & Graybiel, 2016). These parallels raise an interesting question of how we define responses in these tasks: are they goal oriented or are they under habitual control? I address this in the next section.

2.3 SUMMARY

In summary, behavioural inflexibility is not caused by just one factor. It is very likely that not only are there multiple variables affecting behavioural optimisation, but that they are highly interconnected; for example social learning strategies (when to engage in social learning and from whom to learn (Laland, 2004)) are an extension of learning heuristics and explore versus exploit decision algorithms. These in turn are likely linked to the types of behaviours involved, with behavioural complexity affecting decisions, as well as the use of social information. Both of these are dependent on cognitive resources, such as selective attention to environmental and internal cues signalling the potential cost/benefits of behavioural change (Braet et al., 2009; Hester, Madeley, Murphy, & Mattingley, 2009; Padmala & Pessoa, 2010; Rushworth et al., 2012; Theeuwes, 2010), holding in memory representations of both past and potential behavioural variants, identifying the relevant action sequences, and successfully inhibiting or adding action elements to these sequences.

3. EXPERTISE AND HABIT FORMATION

When a chimpanzee performs a behaviour many times, and reliably exhibits this response, I have commonly referred to this as a prepotent response throughout these studies; however, it may be argued that establishing a high level of prepotency is the same as establishing a habit. Both convey a sense of automaticity, of responding without really thinking about the response itself. However, perseveration in the context of a habit results not from a lack of inhibitory control, but rather because habits are insensitive to outcome.

Are prepotent responses habits? In one sense, this may be the same as asking is solution A learnt through stimulus-response associations. As Heyes (2012) has highlighted, we should be cautious in attributing either insight or associative learning to behaviour when we have no clear evidence either way; but given that much of this thesis focuses on the underlying cognition of behaviour, I will address the possibility that chimpanzees had little insight or understanding of the solutions they were performing, and relied on purely associative learning. This is important because associative learning can lead to habit formation. Within neuroscience, two forms of associative learning are distinguished: action-outcome (A-O) learning, and stimulus response (S-R) learning. The former reflects learning that underlies goal-oriented responding. It is the latter that is associated with habit formation within the historical neuroscientific literature, with agents (commonly rats or monkeys) responding to a stimulus with a set behaviour to obtain a reward. There is no connection between performing the behaviour and this behaviour having an effect on gaining a reward i.e. the outcome (Thorndike 1898). These S-R pathways are thought to be simpler than those needed for A-O learning, involving less computational power. However, the

trade-off is that these S-R associations are not sensitive to reward outcome; indeed, the metric used to establish an S-R association is this insensitivity to reward depreciation.

So, are prepotent responses habits? Solution A was not learnt under the conditions normally needed to form S-R associations. S-R associations are generally learnt within a framework of causal opacity and often under some interval learning schedule which decreases the likelihood of recognising a causal connection between behaviour and outcome. This learning environment is remarkably different from the environments in which Solution A was learnt by participating chimpanzees. Instead, it is more likely, especially in intelligent animals, that if chimpanzees lacked insight, then some form of action-outcome learning (trial and error) was involved. So in this traditional sense of habit formation, prepotent responses studied here are unlikely to have been learnt through an S-R association. However, it may be possible for A-O associations to become more like S-R associations with repeated exposure, leading to habitual behaviours (Balleine & Dickinson, 1998; Smith & Graybiel, 2014, 2016). Smith and Graybiel (2014, pg 4) state

> "Useful hallmarks for the formation of skills and habit-like behaviours include increased speed to start and complete tasks, more stereotypic and routed movements through a task environment, fewer deliberations at decision points, reduced distractibility, indifference to negative feedback, and increased performance accuracy"

Many of these traits mirror skill mastery, making it somewhat difficult to disentangle the difference between expertise and habit. Although the exact mechanisms are still a source of investigation, with increasing practice of a behaviour, neural activity may shift from areas associated with goal-directed behaviour, to those associated with habitual behaviour (Smith & Graybiel, 2016). This is thought to reflect an efficient decision-making framework whereby behaviours are initially learnt through trial and error, which allows flexible responding, but with reliable reinforcement (i.e. reward), come under control of the habit system (See Tricomi, Balleine, & O'Doherty (2009) for an example in humans). This behaviour can be expected to remain under habitual control as long as this response is at least partially reinforced (note that both Biways and Pitfall experiments saw behavioural change even when Solution A was reinforced). This may serve to reduce the computational demand of behaviours, as the relationships between actions and outcomes (A-O responding) no longer have to be held in working memory; instead the presentation of the problem itself (the stimulus, or cue) leads to an automatic response, with no representation of the underlying associations between actions and

their effects required (S-R like responding). However, it seems to me we might expect crucial differences between behaviours which are learnt through S-R associations versus those which are first learnt through A-O associations, but become more like S-R behaviours: If a behaviour learnt through trial and error becomes habitual, it is unclear whether this sort of 'habit' would be insensitive to outcome, or for how long this insensitivity would be expected to last (Eric Bowman, personal communication). As Solution A was not learnt under S-R associative learning, what then happens to the action-outcome associations if a behaviour does progress to becoming habitual? Is it simply lost? It seems this would be unlikely. My own way of thinking is focused through the often used example of being on 'automatic pilot' when driving along a familiar route (Solution A); we may have decided that we needed to take a detour along this route for some reason beforehand (Solution B). What is not uncommon though is that when we end up travelling along the familiar route, and upon coming to the crucial junction, we take the most familiar turn (A), and not the one required for our detour (B). This is similar to a habit, where we have disengaged with the intricacies of the task, and rely on a well-rehearsed pathway. However, once we realise an error has been made, we re-engage with the elements of the travel route, and can easily correct our behaviour. Put another way, although we may be acting automatically, this does not mean that we forget action-outcome associations, or that we cannot re-engage these when we become aware that our established solution has yielded a suboptimal outcome (See Daw, Niv, & Dayan, 2005; O'Doherty, Cockburn, & Pauli, 2017).

3.1 SUMMARY

These are important considerations as a main argument of mine is that cognitive load affects behavioural optimisation through detracting from resources required for inhibition of a prepotent response, and this is responsible for behavioural conservatism/perseveration. In contrast, habit formation reduces the cognitive load of behaviours, by, for example, chunking complex action sequences into a single executable unit (Graybiel, 1998). This suggests that complexity of behaviour affects behavioural optimization not because of limited cognitive resources per se, but rather because habit formation reduces cognitive resource use by making complex behaviour less computationally demanding. The cost of reducing computation cost could potentially be insensitivity to suboptimal outcomes marked by perseveration. As discussed in Chapter 5, while I cannot necessarily rule out that solution A has become habitual, flexible use of multiple solution variants as well as predominant use of only outcome relevant actions indicates behaviour is goal-oriented. However even if behaviour had become habitual, it is unclear whether this sort of habit would be insensitive to outcome, nor that we cannot

subsequently re-engage A-O associations when we become aware that our established solution is suboptimal. Once these are re-engaged, we are potentially back to our initial interpretation of complexity of solutions impacting on behavioural optimisation through cognitive load (see also Marcovitch & Zelazo, 2009 for a related account of competing systems). However, the neural underpinnings of decision-making and habit formation is a complex and evolving field, with much research still needed to clarify how habit systems and goal-oriented systems interact (Smith & Graybiel, 2014, 2016). Indeed, one of the most heavily researched brain areas in goal-directed behaviour is the prefrontal Cortex (PFC), which is thought to be at the centre of cognitive control.

4. THE DEVELOPMENT OF COGNITIVE CONTROL

Due to its unique patterns of connectivity with many key regions of the brain, the PFC is thought to have "the ideal infrastructure for synthesising the diverse range of information needed for complex behaviour" (Miller, 2000, pg 59). The PFC as the centre of cognitive control, and may heavily influence the allocation of resources to executive functions, which increasingly come under top-down control with age (Best & Miller, 2010; Braet et al., 2009; Thompson-schill, Ramscar, & Chrysikou, 2009). Specifically, it is suggested that such top-down control is needed to override exploitative behaviours; that is, inhibiting the behaviours currently employed (Solution A), to enable more appropriate responses (Solution B) (Cohen et al., 2007; Daw et al., 2006; Miller & Cohen, 2001). Crucially, the PFC is implicated in inhibitory processes when working memory demand is high (Reynolds, O'Reilly, Cohen, & Braver, 2012; Simmonds, Pekar, & Mostofsky, 2008). This would tie in with studies which suggest not only that response prepotency affects behaviour optimisation due to difficulties with inhibiting the exploit response, but so too does complexity (See Chambers et al., 2009 for a review). The demand placed on PFC resources may make it more difficult for top-down processes to override the exploitative tendency, resulting in perseveration. Thus when the PFC is not yet at full capacity, such as in children, perseveration is quite likely as there is limited control exerted over cognition and behaviour. Conversely, in certain circumstances where behavioural responses are not already tied too closely to a known solution (Defeyter & German, 2003), or under conditions of pedagogy (Bonawitz et al., 2011; Csibra & Gergely, 2011; Wood, Kendal, & Flynn, 2013), this lack of control can actually afford greater flexibility.

This highlights an important potential trade-off between weak and strong cognitive control: increased cognitive control allows for behavioural optimisation because it is associated with greater cognitive capacity in working memory and inhibition (e.g. Diamond & Doar, 1988), allowing the successful inhibition of suboptimal responses, and the subsequent enactment of

more optimal ones. That is, one of the main roles of the PFC is providing top-down control over behaviour, and specifically arbitrating between responses. However, as mentioned in Chapter 2, increased cognitive control also appears to be associated with decreased creative thinking (Chrysikou et al., 2013; Gopnik, Griffiths, & Lucas, 2015; Thompson-schill et al., 2009), as well as negatively interfering with learning (Doll, Hutchison, & Frank, 2011). This is likely due to top-down processing biasing cognition based on prior experience (Miller & Cohen, 2001). While this is an efficient problem solving strategy for the most part, and characterises complex cognition, relying on prior knowledge to guide behaviour (considered an exploit decision) may result in suboptimal use of external information. This external information may be capitalised on by agents engaging in exploratory strategies, such as novices (Luchins, 1942; Wiley, 1998), or those with compromised (Chrysikou et al., 2013) or limited cognitive control (Defeyter & German, 2003). For example, while young children may not effectively use prior information to guide learning, a largely inefficient strategy in complex problem solving, it may be the very thing that allows them to acquire the foundational skills and knowledge that adult cognition is built upon, for example, language competence (Romberg & Saffran, 2010).

As highlighted by Diamond (2013), a lack of creative thinking may be more closely linked to that of task switching or shifting, than difficulties with inhibition per se. This makes sense if we assume there may be some inverse relationship between inhibition and working memory, with task switching, such that with increasing cognitive control, there are differential effects on these executive functions. In this vein, controlling for age, Blackwell, Chatham, Wiseheart, & Munakata (2014) found evidence that those children who switched on a card sorting task - where children are initially asked to sort cards along one dimensions (e.g. shape) before being asked to sort along another dimension (e.g. colour) - had better working memory than those who perseverated. So far, this picture fits well with the pattern of flexibility being underlain by cognitive resource availability; however, there appears to be a developmental period in children where inhibition and task switching exhibit this inverse relationship, with stronger inhibitory control on a card sorting task linked to weaker task switching performance on a Go/No go task (Blackwell & Munakata, 2014). These authors suggest that children who switch may be attempting to proactively remember relevant information, which gives them an advantage in switching tasks (as they remember the new rule/solution). This is computationally demanding and is likely an emerging ability that is correlated with an increase in cognitive capacity (Braver, 2012). In contrast, perseverators may rely on a reactive memory strategy, only recalling information on the spot when presented with cues. In a cord sorting task, there may be a lack of specificity about

which cue is associated with which rule, leading to poor performance (Blackwell et al., 2014; Chatham, Frank, & Munakata, 2009). However, on tasks which involve holding in mind multiple rules (such as Go/No-go) children who rely on proactive memory (top-down control) may overload their working memory system when trying to maintain and rehearse the different rules for responding or withholding a response. In contrast, as the Go/No-go task has unambiguous cues for going and stopping, reactive children may perform better, showing less perseverative errors and/or quicker reaction times.

It is important to note that this inverse relationship between task-switching and inhibition may be developmental in nature, and that adults often show correlations between inhibition and task switching abilities (e.g. Aron, Robbins, & Poldrack, 2004). However, it has been suggested that this trade-off persists into adulthood, but that it is underlain not by limited cognitive resources, but rather powerful cognitive control: it may be that our ability to store and hold in mind strong representations of goal-directed problem solving strategies slows us down on task switching. Specifically, Herd et al. (2014) proposed while increased cognitive control is associated with both improved performance on inhibition and switching tasks, strength of goal representation negatively impacts upon switching. In this sense, we may be better able to understand how creative thinking is sometimes greater in children than adults. As highlighted in Chapter 2, a lack of creative thinking is not necessarily due to limited inhibition or working memory capacities. Einstellung and functional fixedness are caused by becoming stuck on Solution A and subsequently failing to *generate* Solution B, but should be overcome once the agent has knowledge of B (whereas perseveration occurs despite knowledge of B). It would stand to reason that the stronger the representation of A, the more stuck you are likely to be on it (Herd et al., 2014). Young children, and those with compromised frontal regions, may not represent Solution A with the same veracity as an adult due to limited cognitive control. This decreased cognitive capacity may lead to weaker representations of A, making it less difficult to clear A from mind, and subsequently generate B.

Overall, if we are to consider task switching and inhibition processes as separable components, the prepotency and complexity of A may affect how well an individual can inhibit A, but in addition, the strength with which A and B are represented may also impact upon solution choice. In other words, there may be two ways in which Solution A is affecting behavioural flexibility: (i) Solution A affects the ability to change behaviour due to solution complexity interfering with *inhibition* processes, and/or (ii) the strength with which A is represented may affect the ability to *switch* between solutions.

5. THE EVOLUTION OF COGNITIVE CONTROL

The above considerations make it somewhat difficult to compare cognitive control between chimpanzees and humans, insofar that we cannot say for certain that increases in control are associated with only quantitative increases in cognitive capacity. Evidence suggests that humans undergo key cognitive transitions during development (Munakata, Snyder, & Chatham, 2012), progressing from reactive to proactive control. At this point, it is unclear whether chimpanzees follow the same developmental trajectory as humans. Indeed, it may be that the transitions undergone throughout our development hold the key as to why humans are unique in their cognitive and cultural capacities. If this is true, which part then reflects the adaptation? Is it the fluid, exploratory, bottom-up processing seen in younger children, allowing the extensive acquisition of knowledge (Romberg & Saffran, 2010; Thompson-schill et al., 2009), with the associated difficulties in inhibiting learnt routines and representing goals? Or is it the strong cognitive control of adults that promotes effortful arbitration between competing goals, leading to blocks on creative thinking, but ultimately efficient problem solving and expertise? Do chimpanzees embody either of these or are they somewhere in between, using a mix of reactive and proactive strategies to navigate behaviour? Given that the nature of cognitive control in humans is still unresolved despite extensive research, it seems we are some way from being able to answer these questions. As a first attempt though, I would like to highlight an important consideration: chimpanzees are highly innovative animals (Reader & Laland, 2001), with little evidence so far that they actually show set or fixedness. I would tentatively suggest chimpanzees are similar to young children, exhibiting limited cognitive control over their behaviours, as evidenced by both innovative tendencies, as well as perseveration with learnt routines as a function of prepotency and complexity. The alternative view would be that chimpanzees may have the potential to strongly represent goals, and are more similar to human adults. If this is the case, difficulties with switching to B, instead of inhibiting A, may cause perseveration, and this may be linked to an inability to either clear A from mind, to encode information about solution B, or to arbitrate between solution A and B. In my own work, response prepotency was always heightened as this better represents the investment made in cultural behaviours, and moreover, if a response is not prepotent, what exactly is being inhibited? This leads to the interesting question of how to disentangle the effects of response prepotency on inhibition versus the effects of prepotency on task switching. Whether these rely on separable components is at this stage unclear, but we should consider my results are complicated by the strength with which Solution A is represented. However, I remain unsure how solution complexity would impact upon goal

representation, and if we might expect to see the pattern of contextual chimpanzee flexibility I have outlined throughout my thesis if we were to attribute inflexibility to goal representation.

6. CONCLUSION

Cultural behaviours, especially with regards to technologies like those of wild chimpanzees, can be complex in nature (Boesch, Head, & Robbins, 2009; Sanz, Schöning, & Morgan, 2010). Cumulative change in these behaviours typically involves an increase in complexity, and outside of our own hominin line, such cumulative complexity is rare. My findings suggest that this may be caused in part by difficulties in relinquishing complex behaviours, or interrupting the sequence of complex routines. Furthermore, they indicate that high levels of conservatism are to be expected when behavioural optimization involves not only the partial inhibition of a complex solution but also the addition of a complex element to this solution.

Taken together, and along with previous research, my results suggest that chimpanzee conservatism is in part caused by the complexity of behaviour concerned. I propose complexity affects behavioural optimisation through both Hypotheses 1 and 2. Complex behaviours tax limited cognitive resources, placing demands on working memory making it difficult to inhibit a prior solution (A). This is supported by findings that chimpanzees have compromised inhibitory control (Chapter 4: A not B), and more clearly by findings whereby naïve participants readily converge on B, but those with a complex prior solution perseverate with A (Chapter 5: Biways and Pitfall). Thus I propose that having a prior solution affects behavioural optimisation and this is linked to cognitive resource availability (Hypothesis 1). However, the level of perseveration is further heightened when solution B is itself complex. I suggest it is when both solution A and B are complex, and when solution A is highly prepotent, that such behaviours are the most relevant to the study of cumulative culture. This heightened perseveration is likely for several reasons, with the need to inhibit a complex solution, as well as learn a complex alternative, placing yet higher demands on resources, and likely posing a cognitive challenge to chimpanzees (Chapter 6). The complexity of solution B may also militate against the decision to engage in the potentially lengthy trial and error learning needed for skill mastery. Further, the heuristics and mechanism underling the extent to which social information is capitalized upon may also affect the ability to adopt a complex solution B. These latter two considerations are in line with Hypothesis 2, and indicate that having a prior solution in and of itself is not the only reason as to why chimpanzees have limited or no cumulative culture.

Given that chimpanzees are arguably amongst the smartest of non-human primates, we might consider that other species, with more limited cognitive resources than a chimpanzee, would face even greater challenges than chimpanzees on similar tasks of behavioural change. While there have been comparative works completed explicitly examining behavioural flexibility through puzzlebox tasks in a range of primates (e.g. Huebner & Fichtel 2015; Manrique and Call, 2015), the literature does not currently allow as extensive as a review for other primates as I have carried out in this thesis. It would be of great interest to begin testing other species on a range of behavioural flexibility tasks, especially with regards to abandoning a complex Solution A for a simple Solution B. It may be that chimpanzees and humans uniquely share similar executive function processes which give rise to the pattern of contextual flexibility presented throughout this thesis; or it may be that cognitive resources are a universal limiting factor on behavioural flexibility, and consequently, the evolution of cumulative culture.

Notwithstanding other vital socio-cognitive adaptations, it is important to consider that whilst chimpanzees may possess some cognitive functions homologous with our own (Beran et al., 2016; Carruthers, 2013; Inoue & Matsuzawa, 2007; Manrique & Call, 2015; Martin-Ordas, Haun, Colmenares, & Call, 2010; Osvath, Kabadayi, & Jacobs, 2014; Osvath & Osvath, 2008; Vlamings et al., 2009), it is very likely that humans have a greater ability to hold on to and manipulate more information in working memory (Coolidge & Wynn, 2005; Haidle, 2010; see also Washburn, 2016), whether resulting from quantitative or qualitative changes in cognitive control. Thus, not only can humans learn more complex sequences of behaviour, but have more resources available to facilitate behavioural flexibility. I tentatively suggest that chimpanzees may be child-like in their cognitive control, exhibiting perseveration as a result of limited cognitive resources in key executive functions. Like the weak cognitive control exhibited by children, what may appear to be a suboptimal version of a yet to be actualised system may actually be a highly adaptive framework. However, instead of weak cognitive control necessarily being adaptive in that it promotes creative thinking or language acquisition as in children, by considering conservatism from the perspective of expertise, it is easier to see how continually exploiting a known solution may be adaptive: it allows experts to efficiently navigate the problem, applying skills to find a solution that may be outside of the novice's capability. With complex solutions, involving hard won expertise, we might expect there to have been long periods of learning, and thus large investments in this known solution. While innovation may be common in chimpanzees, even exhibiting a human like progression from highly exploratory young to more reserved adults (Reader & Laland, 2001), exploring for a new solution when you already have

one may be a largely inefficient strategy. In this sense, we can perhaps understand why selection has not necessarily favoured strong control in chimpanzees. Unlike our own nomadic hominin ancestors, chimpanzees live in relatively stable environments (and this is likely true of their ancestors), perhaps militating against the pressures needed for the expensive cognitive machinery underlying complex control, with subsequent impacts on cumulative cultural ability.

At some point within our distinct hominin evolutionary past, our ancestors may have overcome a conservative tendency, engaging in exploration, creating new technologies and accumulated artefacts, adaptively employing behavioural flexibility to relinquish, modify and adopt solutions. This may have initially been facilitated through recombination of existing skills and technology "creating innovations without invention, creativity or trial and error learning" (Muthukrishna et al., 2014, pg 5). Thus accumulation may have originated through a mechanism which ultimately reduced the costs of exploration, with these more complex behaviours creating selection for a suite of other adaptive functions (Boyd & Richerson, 1985; Herrmann, Call, Hernàndez-Lloreda, Hare, & Tomasello, 2007; Moll & Tomasello, 2007; Pradhan, Tennie, & van Schaik, 2012; Reader, Hager, & Laland, 2011; van Schaik & Burkart, 2011; Whiten, Hinde, Laland, & Stringer, 2011; Whiten & van Schaik, 2007). Given what we know about modern humans, in an increasingly complex world, selection may have favoured a developmental trajectory that initially affords flexible learning vital to the acquisition of core information or constructs, (Gopnik et al., 2015; Thompson-schill et al., 2009), such as language (Romberg & Saffran, 2010), perhaps capitalising on an already existent system shared with a common ancestor with chimpanzees. This then gives way to a more tightly controlled problem solving framework (Munakata et al., 2012). This heightened cognitive control ultimately allows for the efficient acquisition, arbitration and use of information, which may be necessary for the complex problem solving inherent to true technological accumulation.

Table 1

Summary of research findings

Chapter - Study	Solution A		Action on A	Solution B	Conservatism	Hypothesis
5 - Biways	Prepotent	Simple	Inhibit	Simple	Low	-
5 – Pitfall (Study 2.1)	Prepotent	Complex	Build	Complex	Low	-
5 – Pitfall (Study 2.2)	Prepotent	Complex	Inhibit	Simple	Moderate	1
6 - Serialbox	Prepotent	Complex	Inhibit/Build	Complex	High	1 & 2

Solution A: Original solution used with two levels, Solution A prepotency, and Solution A complexity. Action on A: describes if Solution A needed to be inhibited and/or built upon to use Solution B. Solution B: Solution B complexity. Conservatism gives a basic description of how readily chimpanzees changed behaviours, with low levels of conservatism linked to high behavioural flexibility and high levels of conservatism linked with marked perseveration with Solution A. Hypothesis is which hypothesis I interpret these results to lend support to

REFERENCES

Arbilly, M., & Laland, K. N. (2017). The magnitude of innovation and its evolution in social animals. *Proceedings of the Royal Society of London B: Biological Sciences*, *284*(1848). https://doi.org/10.1098/rspb.2016.2385

Aron, A. R., Robbins, T. W., & Poldrack, R. a. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, *8*(4), 170–7. https://doi.org/10.1016/j.tics.2004.02.010

Amici, F., Aureli, F., & Call, J. (2008). Fission-Fusion Dynamics, Behavioral Flexibility, and Inhibitory Control in Primates. *Current Biology, 18*(18), 1415–1419. https://doi.org/10.1016/j.cub.2008.08.020

Asch, S. E. (1956). Studies of independence and conformity: I. A minority of one against a unanimous majority. *Psychological Monographs: General and Applied*, *70*(9), 1–70.

Baird, A., Kagan, J., Gaudette, T., Walz, K., Hershlag, N., & Boas, D. (2002). Frontal Lobe Activation during Object Permanence: Data from Near- Infrared Spectroscopy. *Neuroimage, 16*(4), 1120. https://doi.org/10.1006/nimg.2002.1170

Balleine, B. W., & Dickinson, A. (1998). Goal-directed instrumental action: Contingency and incentive learning and their cortical substrates. *Neuropharmacology*, *37*(4–5), 407–419. https://doi.org/10.1016/S0028-3908(98)00033-1

Ban, S. D., Boesch, C., & Janmaat, K. R. L. (2014). Tai chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal Cognition, 17*(6), 1353–1364. https://doi.org/10.1007/s10071-014-0771-y

Bar-Yosef, O. (2007). The Upper Paleolithic revolution. *Annu. Rev. Anthropol.*, *31*, 363–393. https://doi.org/10.1177/0392192107076869

Barber, A. D., Caffo, B. S., Pekar, J. J., & Mostofsky, S. H. (2013). Effects of working memory demand on neural mechanisms of motor response selection and control. *Journal of Cognitive Neuroscience 25*(8), 1235 – 1248. doi:10.1162/jocn_a_00394

Bari, A., & Robbins, T. W. (2013). Inhibition and impulsivity: behavioral and neural basis of response control. *Progress in Neurobiology,* 108, 44–79. https://doi.org/10.1016/j.pneurobio.2013.06.005

Baron-Cohen, S. (1998). Does the study of autism justify minimalist innate modularity? *Learning and Individual Differences*, *10*, 180-191.

Barrett, H. C., & Kurzban, R. (2006). Modularity in cognition: Framing the debate. Psychological Review, 113, 628–647.

Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes, Pan paniscus, Gorilla gorilla, and Pongo pygmaeus*) and young children (Homo sapiens). Journal of Experimental Psychology: *Animal Behavior Processes*, 32(3), 239–252. https://doi.org/10.1037/0097-7403.32.3.239

Beilock, S. L., & Decaro, M. S. (2007). From poor performance to success under stress: working memory, strategy selection, and mathematical problem solving under pressure. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 33*(6), 983–98. https://doi.org/10.1037/0278-7393.33.6.983

Bélanger, S., & Belleville, S. (2009). Semantic inhibition impairment in mild cognitive impairment: A distinctive feature of upcoming cognitive decline? *Neuropsychology, 23*(5), 592–606.

Bell, M. A., Wolfe, C. D., & Adkins, D. R. (2007). Frontal lobe development during infancy and childhood. In D. J. Coch, K. W. Fischer, & G. Dawson (Eds.), *Human behavior learning, and the developing brain: Typical development* (pp. 247–276). New York: Guilford.

Beran, M. J. (2015). The comparative science of self-control□: what are we talking about? *Frontiers in Psychology, 6*(January), 1–4. https://doi.org/10.3389/fpsyg.2015.00051

Beran, M. J., & Evans, T. A. (2009). Delay of gratification by chimpanzees (Pan troglodytes) in working and waiting situations. *Behavioural Processes*, *80*(2), 177–81. https://doi.org/10.1016/j.beproc.2008.11.008

Beran, M. J., Evans, T. A, Paglieri, F., McIntyre, J. M., Addessi, E., & Hopkins, W. D. (2014). Chimpanzees (Pan troglodytes) can wait, when they choose to: a study with the hybrid delay task. Animal Cognition, 17(2), 197–205. https://doi.org/10.1007/s10071-013-0652-9

Beran, M. J., Menzel, C. R., Parrish, A. E., Perdue, B. M., Sayers, K., Smith, J. D., & Washburn, D. A. (2016). Primate cognition: attention, episodic memory, prospective

memory, self-control, and metacognition as examples of cognitive control in nonhuman primates. *Wiley Interdisciplinary Reviews: Cognitive Science*, *7*(5), 294–316.

Beran, M. J., Washburn, D. A, & Rumbaugh, D. M. (2007). A Stroop-like effect in color-naming of color-word lexigrams by a chimpanzee (Pan troglodyte). *The Journal of General Psychology*, *134*(2), 217–28. https://doi.org/10.3200/GENP.134.2.217-228

Berger, S. E. (2004). Demands on finite cognitive capacity cause infants' perseverative errors. *Infancy, 5*, 217–238.

Berger, S. E. (2010). Locomotor expertise predicts infants' perseverative errors. Developmental Psychology, 46(2), 326–336. https://doi.org/10.1037/a0018285

Berl, R. E. W., & Hewlett, B. S. (2015). Cultural variation in the use of overimitation by the Aka and Ngandu of the Congo Basin. *PloS One*, *10*(3), e0120180. https://doi.org/10.1371/journal.pone.0120180

Best, J. R., & Miller, P. H. (2010). *A Developmental Perspective on Executive Function, 81*(6), 1641–1660.

Bilalić, M., McLeod, P., & Gobet, F. (2008). Inflexibility of experts-Reality or myth? Quantifying the Einstellung effect in chess masters. *Cognitive Psychology, 56*(2), 73–102. https://doi.org/10.1016/j.cogpsych.2007.02.001

Bilalić, M., McLeod, P., & Gobet, F. (2008b). Why good thoughts block better ones: The mechanism of the pernicious Einstellung (set) effect. *Cognition*, *108*(3), 652–661. https://doi.org/10.1016/j.cognition.2008.05.005

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C., & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, *6*(4), 213–23. https://doi.org/10.1007/s10071-003-0183-x

Bishop, D. V. M. (1997). Cognitive neuropsychology and developmental disorders: Uncomfortable bedfellows. *The Quarterly Journal of Experimental Psychology, 50,* 899-923.

Bjorklund, D. F. (2006). Mother knows best: Epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Developmental Review*, *26*(2), 213–242.

https://doi.org/10.1016/j.dr.2006.02.007

Bjorklund, D. F., & Harnishfeger, K. K. (1990). The ressources construct in cognitive development: Diverses sources of evidence and theory of inefficient inhibition. *Developmental Review*, *10*, 48–71.

Blackwell, K. A., Chatham, C. H., Wiseheart, M., & Munakata, Y. (2014). A developmental window into trade-offs in executive function: the case of task switching versus response inhibition in 6-year-olds. *Neuropsychologia*, *62*, 356–364. https://doi.org/10.1016/j.neuropsychologia.2014.04.016

Blackwell, K. A., & Munakata, Y. (2014). Costs and benefits linked to developments in cognitive control. *Developmental Review*, *17*(2), 203–211. https://doi.org/10.1038/jid.2014.371

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour*, *41*(3), 530–532. https://doi.org/10.1016/S0003-3472(05)80857-7

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(2), 82–91. https://doi.org/10.1002/evan.10106

Boesch, C. (2007). What makes us human (Homo sapiens)? The challenge of cognitive cross-species comparison. *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *121*(3), 227–40. https://doi.org/10.1037/0735-7036.121.3.227

Boesch, C., Head, J., & Robbins, M. M. (2009). Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *Journal of Human Evolution*, *56*(6), 560–9. https://doi.org/10.1016/j.jhevol.2009.04.001

Bonawitz, E., Shafto, P., Gweon, H., Goodman, N. D., Spelke, E., & Schulz, L. (2011). The Double-edged Sword of Pedagogy: Instruction limits spontaneous exploration and discovery. *Cognition, 120*(3), 322–330. https://doi.org/10.1016/j.cognition.2010.10.001.

Bonnie, K. E., Horner, V., Whiten, A., & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings. Biological Sciences / The Royal Society*, *274*(1608), 367–72. https://doi.org/10.1098/rspb.2006.3733

Bonnie, K. E., Milstein, M. S., Calcutt, S. E., Ross, S. R., Wagner, K. E., & Lonsdorf, E. V. (2012). Flexibility and persistence of chimpanzee (Pan troglodytes) foraging behavior in a captive environment. *American Journal of Primatology, 74*(7), 661–8. https://doi.org/10.1002/ajp.22020

Botvinick, M. M., & Cohen, J. D. (2014). The computational and neural basis of cognitive control: Charted territory and new frontiers. *Cognitive Science, 38*(6), 1249–1285. https://doi.org/10.1111/cogs.12126

Boudreau, J. P., & Bushnell, E. W. (2000). Spilling thoughts: configuring attentional resources in infants' goal-directed actions. *Infant Behavior and Development, 23*(3–4), 543–566. https://doi.org/10.1016/S0163-6383(01)00059-5

Boyd, R., & Derex, M. (2015). The foundations of the human cultural niche. *Nature Communications*, *6*(May), 1–7. https://doi.org/10.1038/ncomms9398

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: Univesity of Chicago Press.

Boyd, R., & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, *16*(2), 125–143. https://doi.org/10.1016/0162-3095(94)00073-G

Boyd, R., & Richerson, P. J. (1996). Why Culture is Common , but Cultural Evolution is Rare. *Proceedings of the British Academy*, *88*, 77–93.

Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences of the United States of America*, *108 Suppl*, 10918–10925. https://doi.org/10.1073/pnas.1100290108

Braet, W., Johnson, K. A., Tobin, C. T., Acheson, R., Bellgrove, M. a, Robertson, I. H., & Garavan, H. (2009). Functional developmental changes underlying response inhibition and error-detection processes. *Neuropsychologia, 47*(14), 3143–51. https://doi.org/10.1016/j.neuropsychologia.2009.07.018

Brass, M., & Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, *9*(10), 489–495. https://doi.org/10.1016/j.tics.2005.08.007

Britton, B. K., & Tesser, A. (1982). Effects of Prior Knowledge on Use of Cognitive Capacity in Three Complex Cognitive Tasks. *Journal of Verbal Learning and Verbal Behavior, 21*, 421–436.

Brosnan, S. F., & Hopper, L. M. (2014). Psychological limits on animal innovation. *Animal Behaviour*, *92*, 325–332. https://doi.org/10.1016/j.anbehav.2014.02.026

Bunge, S. A., Dudukovic, N. M., Thomason, M. E., Vaidya, C. J., & Gabrieli, J. D. E. (2002). to Cognitive Control in Children : Evidence from fMRI. *Neuron, 33*, 301–311. https://doi.org/10.1016/S0896-6273(01)00583-9

Bunge, S. A., Ochsner, K. N., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (2001). Prefrontal regions involved in keeping information in and out of mind. Brain : *A Journal of Neurology, 124,* 2074–86. https://doi.org/10.1093/brain/124.10.2074

Burke, C. J., Tobler, P. N., Baddeley, M., & Schultz, W. (2010). Neural mechanisms of observational learning. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(32), 14431–14436. https://doi.org/10.1073/pnas.1003111107

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*(4), F31-8. https://doi.org/10.1111/j.1467-7687.2007.00630.x

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2008). Rational tool use and tool choice in human infants and great apes. *Child Development*, *79*(3), 609–26. https://doi.org/10.1111/j.1467-8624.2008.01146.x

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2013). Chimpanzees, Pan troglodytes, recognize successful actions, but fail to imitate them. *Animal Behaviour*, *86*(4), 755–761. https://doi.org/10.1016/j.anbehav.2013.07.015

Byrne, R. W., & Rapaport, L. G. (2011). What are we learning from teaching? *Animal Behaviour*, *82*(5), 1207–1211. https://doi.org/10.1016/j.anbehav.2011.08.018

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: a hierarchical approach. *The Behavioral and Brain Sciences*, *21*(5), 667-84-721. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10097023

Caldwell, C. A. (2015). Learning Strategies and Cultural Evolution during the Palaeolithic,

145–154. https://doi.org/10.1007/978-4-431-55363-2

Caldwell, C. A, & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution. Is imitation necessary? *Psychological Science*, *20*(12), 1478–83. https://doi.org/10.1111/j.1467-9280.2009.02469.x

Caldwell, C. A, Schillinger, K., Evans, C. L., & Hopper, L. M. (2012). End state copying by humans (Homo sapiens): implications for a comparative perspective on cumulative culture. *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *126*(2), 161–9. https://doi.org/10.1037/a0026828

Call, J. (2001). Object permanence in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes), and children (Homo sapiens). *Journal of Comparative Psychology, 115*(2), 159–171. https://doi.org/10.1037//0735-7036.115.2.159

Call, J. (2010). Do apes know that they could be wrong? *Animal Cognition*, *13*(5), 689–700. https://doi.org/10.1007/s10071-010-0317-x

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Animal Cognition*, *8*(3), 151–63. https://doi.org/10.1007/s10071-004-0237-8

Carlson, S. M. (2005). Developmentally sensitive measures of executive function in preschool children. *Developmental Neuropsychology, 28*, 595–616.

Caro, A. T. M., & Hauser, M. D. (1992). Is There Teaching in Nonhuman Animals ? *The Quarterly Review of Biology*, *67*(2), 151–174.

Carr, K., Kendal, R. L., & Flynn, E. G. (2015). Imitate or innovate? Children's innovation is influenced by the efficacy of observed behaviour. *Cognition, 142,* 322–332. https://doi.org/10.1016/j.cognition.2015.05.005

Carruthers, P. (2013). Evolution of working memory. *Proceedings of the National Academy of Sciences*, *110*(Supplement_2), 10371–10378. https://doi.org/10.1073/pnas.1301195110

Castro, L., & Toro, M. A. (2014). Cumulative cultural evolution: the role of teaching. *Journal of Theoretical Biology*, *347*, 74–83. https://doi.org/10.1016/j.jtbi.2014.01.006

Chambers, C. D., Garavan, H., & Bellgrove, M. A. (2009). Insights into the neural basis of response inhibition from cognitive and clinical neuroscience. *Neuroscience and Biobehavioral Reviews, 33*(5), 631–46. https://doi.org/10.1016/j.neubiorev.2008.08.016

Chatham, C. H., Frank, M. J., & Munakata, Y. (2009). Pupillometric and behavioral markers of a developmental shift in the temporal dynamics of cognitive control. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(14), 5529–33. https://doi.org/10.1073/pnas.0810002106

Chmielewski, W. X., Mückschel, M., Stock, A.-K., & Beste, C. (2015). The impact of mental workload on inhibitory control subprocesses. *NeuroImage, 112,* 96–104. https://doi.org/10.1016/j.neuroimage.2015.02.060

Chrysikou, E. G., Hamilton, R. H., Coslett, H. B., Datta, A., Bikson, M., & Thompson-Schill, S. L. (2013). Noninvasive transcranial direct current stimulation over the left prefrontal cortex facilitates cognitive flexibility in tool use. *Cognitive Neuroscience, 4(*2), 81–9. https://doi.org/10.1080/17588928.2013.768221

Chudek, M., Heller, S., Birch, S., & Henrich, J. (2012). Prestige-biased cultural learning: bystander's differential attention to potential models influences children's learning. *Evolution and Human Behavior*, *33*(1), 46–56. https://doi.org/10.1016/j.evolhumbehav.2011.05.005

Clearfield, M. W., Diedrich, F. J., Smith, L. B., & Thelen, E. (2006). Young infants reach correctly in A-not-B tasks: On the development of stability and perseveration. *Infant Behavior and Development*, *29*(3), 435–444. https://doi.org/10.1016/j.infbeh.2006.03.001

Clearfield, M. W., Dineva, E., Smith, L. B., Diedrich, F. J., & Thelen, E. (2009). Cue salience and infant perseverative reaching: tests of the dynamic field theory. *Developmental Science*, *12*(1), 26–40. https://doi.org/10.1111/j.1467-7687.2008.00769.x

Clegg, J. M., & Legare, C. H. (2016). A cross-cultural comparison of children's imitative flexibility. *Developmental Psychology*, *52*(9), 1435–1444. https://doi.org/10.1037/dev0000131

Clement, F., Koenig, M., & Harris, P. (2004). The Ontogenesis of Trust. *Mind & Language*, *19*(4), 360–379.

Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1481), 933–942. https://doi.org/10.1098/rstb.2007.2098

Collette, F., Van Der Linden, M., Laureys, S., Delfiore, G., Degueldre, C., Luxen, A., & Salmon, E. (2005). Exploring the unity and diversity of the neural substrates of executive functioning. *Human Brain Mapping, 25*(4), 409–423. https://doi.org/10.1002/hbm.20118

Conway, A. R., Cowan, N., & Bunting, M. F. (2001). The cocktail party phenomenon revisited: the importance of working memory capacity. *Psychonomic Bulletin & Review, 8*(2), 331–335. https://doi.org/10.3758/BF03196169

Cook, P., & Wilson, M. (2010). Do young chimpanzees have extraordinary working memory? *Psychonomic Bulletin & Review*, *17*(4), 599–600. https://doi.org/10.3758/PBR.17.4.599

Coolidge, F. L., & Wynn, T. (2005). Working Memory, its Executive Functions, and the Emergence of Modern Thinking. *Cambridge Archaeological Journal*, *15*(1996), 5–26. https://doi.org/10.1017/S0959774305000016

Corriveau, K. H., & Harris, P. L. (2010). Preschoolers (sometimes) defer to the majority in making simple perceptual judgments. *Developmental Psychology*, *46*(2), 437–45. https://doi.org/10.1037/a0017553

Cosmides, L., & Tooby, J. (2013). Evolutionary psychology: new perspectives on cognition and motivation. *Annual Review of Psychology*, *64*, 201–29. https://doi.org/10.1146/annurev.psych.121208.131628

Cragg, L., & Nation, K. (2008). Go or no-go? Developmental improvements in the efficiency of response inhibition in mid-childhood. *Developmental Science, 11*(6), 819–827. https://doi.org/10.1111/j.1467-7687.2008.00730.x

Crooks, N. M., & Mcneil, N. M. Increased Practice with " Set " Problems Hinders Performance on the Water Jar Task, 643–648. In N. A. Taatgen & H. van Ri jn (Eds.). (2009). Proceedings of the 31st Annual Conference of the Cognitive Science Society. Austin, TX: Cognitive Science Society.

Csibra, G., & Gergely, G. (2011). Natural pedagogy as evolutionary adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1149–1157.

https://doi.org/10.1098/rstb.2010.0319

d'Errico, F., & Stringer, C. B. (2011). Evolution, revolution or saltation scenario for the emergence of modern cultures? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1060–1069. https://doi.org/10.1098/rstb.2010.0340

de la Torre, I. (2011). The origins of stone tool technology in Africa: a historical perspective. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1028–37. https://doi.org/10.1098/rstb.2010.0350

Davidson, M. C., Amso, D., Anderson, L. C., & Diamond, A. (2006). Development of cognitive control and executive functions from 4 to 13 years: evidence from manipulations of memory, inhibition, and task switching. *Neuropsychologia, 44*(11), 2037–78. https://doi.org/10.1016/j.neuropsychologia.2006.02.006

Davis, S. J., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviors in chimpanzees (Pan troglodytes). *Scientific Reports*, *6*(35953), 1–12. https://doi.org/10.1534/g3.115.019877

Daw, N. D., O'Doherty, J. P., Dayan, P., Dolan, R. J., & Seymour, B. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, *441*(7095), 876–9. https://doi.org/10.1038/nature04766

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the social and cognitive processes underlying human cumulative culture. *Science (New York, N.Y.)*, *335*(6072), 1114–8. https://doi.org/10.1126/science.1213969

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2013). Human cumulative culture: a comparative perspective. *Biological Reviews of the Cambridge Philosophical Society*. https://doi.org/10.1111/brv.12053

Defeyter, M. A., & German, T. P. (2003). Acquiring an understanding of design: evidence from children's insight problem solving. *Cognition, 89*(2), 133–155. https://doi.org/10.1016/S0010-0277(03)00098-2

Dempster, F. N. (1992). The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. *Developmental Review*, *12*, 45–75.

Derex, M., Beugin, M.-P., Godelle, B., & Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature*, *503*(7476), 389–91. https://doi.org/10.1038/nature12774

Derex, M., & Boyd, R. (2015). The foundations of the human cultural niche. *Nature Communications*, *6*(May), 8398. https://doi.org/10.1038/ncomms9398

Derex, M., Feron, R., Godelle, B., & Raymond, M. (2015). Social learning and the replication process : an experimental investigation.

Derex, M., Godelle, B., & Raymond, M. (2012). Social learners require process information to outperform individual learners. *Evolution*, *67*(3), 688–697. https://doi.org/10.5061/dryad.5ck3n

Deutsch, M., & Gerard, H.B. (1955). A study of normative and informational social influences upon individual judgement. *Journal of Abnormal Social Psychology, 51*, 629-636.

Diamond, A. (1985). Development of the ability to use recall to guide action, as indicated by infants' performance on AB. *Child Development 56,* 868–883.

Diamond, A. (1988). Abilities and Neural Mechanisms Underlying AB Performance. *Child Development*, *59*(2), 523–527.

Diamond, A. (2005). Not Quite as Grown-Up as We Like to Think. *Psychological Science, 16*(4), 291–298. https://doi.org/10.1111/j.0956-7976.2005.01530.x

Diamond, A. (2013). Executive functions. *Annual Review of Psychology, 64*, 135–68. https://doi.org/10.1146/annurev-psych-113011-143750

Diamond, A., Cruttenden, L., & Neiderman, D. (1994). AB with multiple wells: 1. Why are multiple wells sometimes easier than two wells? 2. Memory + inhibition? *Developmental Psychology*, *30*(2), 192–205.

Diamond, A., & Doar,B. (1989). The performance of human infants on a measure of frontal cortex function, the delayed response task. *Developmental Psychobiology, 22*, 271–294.

DiYanni, C., & Kelemen, D. (2008). Using a bad tool with good intention: Young children's imitation of adults' questionable choices. *Journal of Experimental Child Psychology, 101*(4), 241–261. https://doi.org/10.1016/j.jecp.2008.05.002

Doll, B. B., Hutchison, K. E., & Frank, M. J. (2011). Dopaminergic genes predict individual differences in susceptibility to confirmation bias. *The Journal of Neuroscience*: The Official Journal of the Society for Neuroscience, 31(16), 6188–6198. https://doi.org/10.1523/JNEUROSCI.6486-10.2011

Enquist, M., & Ghirlanda, S. (2007). Evolution of social learning does not explain the origin of human cumulative culture. *Journal of Theoretical Biology*, *246*(1), 129–35. https://doi.org/10.1016/j.jtbi.2006.12.022

Enquist, M., Ghirlanda, S., & Eriksson, K. (2011). Modelling the evolution and diversity of cumulative culture. Philosophical Transactions of the Royal Society B: Biological Sciences, 366(1563), 412–423. https://doi.org/10.1098/rstb.2010.0132

Enquist, M., Strimling, P., Eriksson, K., Laland, K., & Sjostrand, J. (2010). One cultural parent makes no culture. *Animal Behaviour*, *79*(6), 1353–1362. https://doi.org/10.1016/j.anbehav.2010.03.009

Eriksson, K., Enquist, M., & Ghirlanda, S. (2007). Critical points in current theory of conformist social learning. *Journal of Evolutionary Psychology*, *5*(1), 67–87. https://doi.org/10.1556/JEP.2007.1009

Espy, K. A., Kaufmann, P. M., McDiarmid, M. D., & Glisky, M. L. (1999). Executive Functioning in Preschool Children: Performance on A-Not-B and Other Delayed Response Format Tasks. *Brain and Cognition*, *41*(2), 178–199. https://doi.org/10.1006/brcg.1999.1117

Evans, T. A., Perdue, B., & Beran, M. J. (2014). The Relationship between Event-Based Prospective Memory and Ongoing Task Performance in Chimpanzees (Pan troglodytes). *PLoS ONE*, *9*(11), e112015. https://doi.org/10.1371/journal.pone.0112015

Fang, C., & Levinthal, D. A. (2009). Near-term liability of exploitation: Exploration and exploitation in multistage problems. *Organization Science*, *20*(3), 538–551. https://doi.org/10.1287/orsc.1080.0376

Flynn, E. (2008). Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1509), 3541–51. https://doi.org/10.1098/rstb.2008.0136

Fragazy, D. M. & Perry, S. (Eds). (2003). *The Biology of Traditions: Models and Evidence.* Cambridge, UK: Cambridge University Press

Franks, N. R., & Richardson, T. (2006). Teaching in tandem-running ants. *Nature*, *439*(7073), 153. https://doi.org/10.1038/439153a

Franz, M., & Matthews, L. J. (2010). Social enhancement can create adaptive, arbitrary and maladaptive cultural traditions. *Proceedings. Biological Sciences / The Royal Society*, *277*(1698), 3363–72. https://doi.org/10.1098/rspb.2010.0705

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. *Scientific Reports*, *4*, 1–7. https://doi.org/10.1038/srep05283

Galef, B. G. (1992). The question of animal culture. *Human Nature (Hawthorne, N.Y.)*, *3*(2), 157–78. https://doi.org/10.1007/BF02692251

Galef, B. G. (2015). Laboratory studies of imitation/field studies of tradition: towards a synthesis in animal social learning. *Behavioural Processes*, *112*, 114–9. https://doi.org/10.1016/j.beproc.2014.07.008

Galef, B. G., Jr., & Whiten, A. (2017). The comparative psychology of social learning. In J. Call (Ed.), G. Burghardt, I. Pepperberg, C. Snowdon, & T. Zentall (Assoc. Eds.), *APA Handbook of Comparative Psychology*. pp. 411-440. Washington, DC: American Psychological Association.

Gathercole, S. E., Alloway, T. P., Kirkwood, H. J., Elliott, J. G., Holmes, J., & Hilton, K. A. (2008). Attentional and executive function behaviours in children with poor working memory. *Learning and Individual Differences, 18*(2), 214–223. https://doi.org/10.1016/j.lindif.2007.10.003

Gergely, B. G., Bekkering, H., & Király, I. (2002). Rational imitation in preverbal infants. *Nature*, *415*(6873), 755. https://doi.org/10.1038/415755a

Gergely, A., Compton, A. B., Newberry, R. C., & Miklósi, Á. (2016). Social Interaction with an "unidentified Moving Object" Elicits A-Not-B Error in Domestic Dogs. *PLoS ONE*, *11*(4), 1–12. https://doi.org/10.1371/journal.pone.0151600

German, T. P., & Barrett, H. C. (2005). Functional fixedness in a technologically sparse culture. *Psychological Science, 16*(1), 1–5. https://doi.org/10.1111/j.0956-7976.2005.00771.x

Giraldeau, L.-A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *357*(1427), 1559–66. https://doi.org/10.1098/rstb.2002.1065

Gopnik, A., Griffiths, T. L., & Lucas, C. G. (2015). When Younger Learners Can Be Better (or at Least More Open-Minded) Than Older Ones. Current Directions in *Psychological Science, 24*(2), 87–92. https://doi.org/10.1177/0963721414556653

Grandjean, J., & Collette, F. (2011). Influence of response prepotency strength, general working memory resources, and specific working memory load on the ability to inhibit predominant responses: A comparison of young and elderly participants. *Brain and Cognition, 77*(2), 237–247. https://doi.org/10.1016/j.bandc.2011.08.004

Graybiel, A. M. (1998). The basal ganglia and chunking of action repertoires. Neurobiol. *Learning & Memory*. 70, 119–136. doi: 10.1006/nlme.1998.3843

Gruber, T., Muller, M., & Reynolds, V. (2011). Community-specific evaluation of tool affordances in wild chimpanzees. *Scientific Reports*, *1*(128), Publsihed online 2011 November 3. https://doi.org/10.1038/srep00128

Grusec, J. E., & Hastings, P. D. (2007). *The Handbook of Socialization*: *Theory and research*. New York: Guilford Press

Haidle, M. N. (2010). Working-Memory Capacity and the Evolution of Modern Cognitive Potential. *Current Anthropology*, *51*(s1), S149–S166. https://doi.org/10.1086/650295

Halford, G. S., Wilson, W. H., & Phillips, S. (1998). Processing capacity defined by relational complexity: implications for comparative, developmental, and cognitive psychology. *The Behavioral and Brain Sciences, 21*(6), 803–864. https://doi.org/10.1017/S0140525X98001769

Hanus, D., Mendes, N., Tennie, C., & Call, J. (2011). Comparing the performances of apes (*Gorilla gorilla, Pan troglodytes, Pongo pygmaeus*) and human children (*Homo sapiens*)

in the floating peanut task. *PloS One, 6*(6), e19555. https://doi.org/10.1371/journal.pone.0019555

Harmand, S., Lewis, J. E., Feibel, C. S., Lepre, C. J., Prat, S., Lenoble, A., ... Roche, H. (2015). 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature*, *521*(7552), 310–5. https://doi.org/10.1038/nature14464

Hashimoto, C., Isaji, M., Koops, K., & Furuichi, T. (2015). First records of tool-set use for ant-dipping by Eastern chimpanzees (Pan troglodytes schweinfurthii) in the Kalinzu Forest Reserve, Uganda. *Primates*, *56*(4), 301–305. https://doi.org/10.1007/s10329-015-0478-y

Haun, D. B. M., Rekers, Y., & Tomasello, M. (2012). Majority-biased transmission in chimpanzees and human children, but not orangutans. *Current Biology : CB*, *22*(8), 727–31. https://doi.org/10.1016/j.cub.2012.03.006

Haun, D. B. M., Rekers, Y., & Tomasello, M. (2014). Children conform to the behavior of peers; other great apes stick with what they know. *Psychological Science*, *25*(12), 2160–7. https://doi.org/10.1177/0956797614553235

Haun, D. B. M., & Tomasello, M. (2011). Conformity to peer pressure in preschool children. *Child Development*, *82*(6), 1759–67. https://doi.org/10.1111/j.1467-8624.2011.01666.x

Henrich, J. (2004). Demography and cultural evolution: How adaptive cultural processes can produce maladaptive losses: The Tasmanian case. *American Antiquity*, *69*(2), 197–214.

Henrich, J. (2015). *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (New Jersey: Princeton University Press).

Henrich, J., & Boyd, R. (1998). The Evolution of Conformist Transmission and the Emergence of Between-Group Differences. *Evolution and Human Behavior*, *19*(4), 215–241. https://doi.org/10.1016/S1090-5138(98)00018-X

Henrich, J., & Boyd, R. (2001). Why people punish defectors. Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*, *208*(1), 79–89. https://doi.org/10.1006/jtbi.2000.2202

Henrich, J., & Gil-White, F. J. (2001). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human*

Behavior : Official Journal of the Human Behavior and Evolution Society, *22*(3), 165–196. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11384884

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, *33*, 61–135. https://doi.org/10.1017/S0140525X0999152X

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(3), 123–135. https://doi.org/10.1002/evan.10110

Herd, S. A., Reilly, R. C. O., Hazy, T. E., Chatham, C. H., Brant, A. M., & Friedman, N. P. (2014). A neural network model of individual differences in task switching abilities. *Neuropsychologia, 62*, 375–389. https://doi.org/10.1016/j.neuropsychologia.2014.04.014

Herrmann, E., Call, J., Hernández-lloreda, M. V., Hare, B., & Tomasello, M. (2007). Humans Have Evolved Specialized Skills of Social Cognition : The Cultural Intelligence Hypothesis, *Science*, *317*(5843), 1360–1366.

Hester, R., & Garavan, H. (2005). Working memory and executive function: the influence of content and load on the control of attention. *Memory & Cognition, 33*(2), 221–233. https://doi.org/10.3758/BF03195311

Hester, R., Murphy, K., & Garavan, H. (2004). Beyond common resources: The cortical basis for resolving task interference. *NeuroImage, 23*(1), 202–212. https://doi.org/10.1016/j.neuroimage.2004.05.024

Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter-gatherers. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1168–78. https://doi.org/10.1098/rstb.2010.0373

Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *69*(2), 207–31. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/8054445

Heyes, C. M. (2012). Simple minds: a qualified defence of associative learning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1603), 2695–2703. https://doi.org/10.1098/rstb.2012.0217

Heyes, C. M. & Galef, B. G. (1996) *Social Learning in Animals: The Roots of Culture*. Amsterdam: Elsevier

Hill, K. R., Wood, B. M., Baggio, J., Hurtado, A. M., & Boyd, R. T. (2014). Hunter-gatherer inter-band interaction rates: Implications for cumulative culture. *PLoS ONE*, *9*(7). https://doi.org/10.1371/journal.pone.0102806

Hobaiter, C., & Byrne, R. W. (2010). Able-bodied wild chimpanzees imitate a motor procedure used by a disabled individual to overcome handicap. *PloS One*, *5*(8), e11959. https://doi.org/10.1371/journal.pone.0011959

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology*, *12*(9), e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W., ... Hill, C. M. (2015). Apes in the Anthropocene: flexibility and survival. *Trends in Ecology & Evolution*, *30*(4), 215–22. https://doi.org/10.1016/j.tree.2015.02.002

Holmes, P., & Cohen, J. D. (2014). Optimality and some of its discontents: Successes and shortcomings of existing models for binary decisions. *Topics in Cognitive Science*, *6*(2), 258–278. https://doi.org/10.1111/tops.12084

Hopkins, W. D., Russell, J. L., & Schaeffer, J. (2014). Chimpanzee Intelligence Is Heritable. *Current Biology*, *24*(14), 1649–1652. https://doi.org/10.1016/j.cub.2014.05.076

Hopper, L. M., Kurtycz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: a test of problem solving, flexibility, and spatial discounting. *PeerJ*, *3*, e833. https://doi.org/10.7717/peerj.833

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through "ghost" conditions. *Proceedings. Biological Sciences / The Royal Society*, *275*(1636), 835–40. https://doi.org/10.1098/rspb.2007.1542

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2015). The importance of witnessed agency in chimpanzee social learning of tool use. *Behavioural Processes*, *112*, 120–129. https://doi.org/10.1001/jamasurg.2014.1086.Feasibility

Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially

maintained food preferences indicate both conservatism and conformity. *Animal Behaviour*, *81*(6), 1195–1202. https://doi.org/10.1016/j.anbehav.2011.03.002

Hopper, L., Spiteri, a, Lambeth, S., Schapiro, S., Horner, V., & Whiten, a. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour*, *73*(6), 1021–1032. https://doi.org/10.1016/j.anbehav.2006.07.016

Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., & Laland, K. N. (2008). Lessons from animal teaching. *Trends in Ecology and Evolution*, *23*(9), 486–493. https://doi.org/10.1016/j.tree.2008.05.008

Hoppitt, W. & Laland, K. (2013). *Social Learning: An Introduction to Mechanisms, Methods, and Models*. Princeton: Princeton University Press.

Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PloS One*, *5*(5), e10625. https://doi.org/10.1371/journal.pone.0010625

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*(3), 164–81. https://doi.org/10.1007/s10071-004-0239-6

Horner, V., Whiten, A., Flynn, E., & de Waal, F. B. M. (2006). Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(37), 13878–83. https://doi.org/10.1073/pnas.0606015103

Houghton, G., & Tipper, S. P. (1994). A model of inhibitory mechanisms in selective attention. In D. Dagenbach & T. H. Carr (Eds.), *Inhibitory processes in attention, memory, and language*

Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes). Animal Cognition, 12*(2), 209–16. https://doi.org/10.1007/s10071-008-0183-y

Huebner, F., & Fichtel, C. (2015). Innovation and behavioral flexibility in wild redfronted lemurs (*Eulemur rufifrons*). *Animal Cognition, 18*(3), 777–87. https://doi.org/10.1007/s10071-015-0844-6

Humle, T., & Matsuzawa, T. (2002). Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. *American Journal of Primatology*, *58*(3), 133–48. https://doi.org/10.1002/ajp.10055

Humle, T., Snowdon, C. T., & Matsuzawa, T. (2009). Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition*, *12 Suppl 1*, S37-48. https://doi.org/10.1007/s10071-009-0272-6

Inoue, S., & Matsuzawa, T. (2007). Working memory of numerals in chimpanzees. *Current Biology*, *17*(23), 1004–1005.

Isler, K., & Van Schaik, C. P. (2014). How humans evolved large brains: Comparative evidence. *Evolutionary Anthropology*, *23*(2), 65–75. https://doi.org/10.1002/evan.21403

Jordan, P. L., & Morton, J. B. (2012). Perseveration and the status of 3-year-olds' knowledge in a card-sorting task: evidence from studies involving congruent flankers. *Journal of Experimental Child Psychology, 111*(1), 52–64. https://doi.org/10.1016/j.jecp.2011.06.011

Kane, M. J., & Engle, R. W. (2003). Working-memory capacity and the control of attention: The contributions of goal neglect, response competition, and task set to Stroop interference. *Journal of Experimental Psychology: General, 132*(1), 47–70. https://doi.org/10.1037/0096-3445.132.1.47

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. *Trends in Cognitive Sciences, 2,* 389-398.

Karmiloff-Smith, A. (2009a) Nativism versus neuroconstructivism: Rethinking the study of developmental disorders. *Developmental Psychology*, *45*, 56-63

Karmiloff-Smith, A. (2009b). Preaching to the converted: from constructivism to neuroconstructivism. *Child Development Perspectives, 3,* 99-102.

Kempe, M., & Mesoudi, A. (2014). An experimental demonstration of the effect of group size on cultural accumulation. *Evolution and Human Behavior*. https://doi.org/10.1016/j.evolhumbehav.2014.02.009

Kenward, B., Karlsson, M., & Persson, J. (2011). Over-imitation is better explained by norm learning than by distorted causal learning. *Proceedings. Biological Sciences / The Royal Society*, *278*(1709), 1239–46. https://doi.org/10.1098/rspb.2010.1399

Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J., & Hoppitt, W. (2015). Chimpanzees copy dominant and knowledgeable individuals: Implications for cultural diversity. *Evolution and Human Behavior, 36*,65–72.

Kirkham, N. Z., Cruess, L., & Diamond, A. (2003). Helping children apply their knowledge to their behavior on a dimension-switching task. *Developmental Science, 6*(5), 449–467. https://doi.org/10.1111/1467-7687.00300

Kline, M. A. (2014). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences*, (January), 1–70. https://doi.org/10.1017/S0140525X14000090

Koops, K., McGrew, W. C., & Matsuzawa, T. (2013). Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, Pan troglodytes verus? *Animal Behaviour*, *85*(1), 175–185. https://doi.org/10.1016/j.anbehav.2012.10.022

Knoblich, G., Ohlsson, S., & Raney, G. E. (2001). An eye movement study of insight problem solving. *Memory & Cognition, 29*(7), 1000–1009.

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, *32*(1), 4–14.

Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(3), 150–159. https://doi.org/10.1002/evan.10111

Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*(10), 542–7. https://doi.org/10.1016/j.tree.2006.06.005

Laland, K. N., Odling-Smee, J., & Myles, S. (2010). How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews. Genetics*, *11*(2), 137–48. https://doi.org/10.1038/nrg2734

Langergraber, K. E., Boesch, C., Inoue, E., Inoue-Murayama, M., Mitani, J. C., Nishida, T., ... Vigilant, L. (2011). Genetic and "cultural" similarity in wild chimpanzees. *Proceedings. Biological Sciences / The Royal Society*, *278*(1704), 408–16. https://doi.org/10.1098/rspb.2010.1112

Langergraber, K. E., & Vigilant, L. (2011). Genetic differences cannot be excluded from generating behavioural differences among chimpanzee groups. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1715), 2094–2095.

https://doi.org/10.1098/rspb.2011.0391

Lazer, D., & Friedman, A. (2007). The network structure of exploration and exploitation. *Administrative Science Quarterly*, *52*, 667–694.

Legare, C. H., & Nielsen, M. (2015). Imitation and Innovation: The Dual Engines of Cultural Learning. *Trends in Cognitive Sciences*, *19*(11), 688–699. https://doi.org/10.1016/j.tics.2015.08.005

Lehner, S. R., Burkart, J. M., & Schaik, C. P. Van. (2011). Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques? *Journal of Comparative Psychology (Washington, D.C. : 1983)*, *125*(4), 446–55. https://doi.org/10.1037/a0024413

Lewis, H. M., & Laland, K. N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1599), 2171–80. https://doi.org/10.1098/rstb.2012.0119

Lewis, J. E., Harmand, S., Harmand, S., Leakey, L., Tobias, P., Napier, J., ... Fragaszy, D. (2016). An earlier origin for stone tool making: implications for cognitive evolution and the transition to Homo. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *371*(1698), 310–315. https://doi.org/10.1098/rstb.2015.0233

Luchins, A. S. (1942). Mechanization in problem solving: The effect of Einstellung. *Psychological Monographs* (6, Whole No. 248).

Luncz, L. V, & Boesch, C. (2014). Tradition over trend: Neighboring chimpanzee communities maintain differences in cultural behavior despite frequent immigration of adult females. *American Journal of Primatology*, (October 2013). https://doi.org/10.1002/ajp.22259

Luncz, L. V, & Boesch, C. (2015). The extent of cultural variation between adjacent chimpanzee (Pan troglodytes verus) communities; a microecological approach. *American Journal of Physical Anthropology*, *156*(1), 67–75. https://doi.org/10.1002/ajpa.22628

Luncz, L. V, Mundry, R., & Boesch, C. (2012). Evidence for cultural differences between neighboring chimpanzee communities. *Current Biology : CB*, *22*(10), 922–6. https://doi.org/10.1016/j.cub.2012.03.031

Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M., & Keil, F. C. (2011). The scope and limits of overimitation in the transmission of artefact culture. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1158–67. https://doi.org/10.1098/rstb.2010.0335

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19751–6. https://doi.org/10.1073/pnas.0704452104

Ma, L., & Ganea, P. A. (2010). Dealing with conflicting information: Young children's reliance on what they see versus what they are told. *Developmental Science*, *13*(1), 151–160. https://doi.org/10.1111/j.1467-7687.2009.00878.x

MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., ... Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America, 111*(20), E2140-8. https://doi.org/10.1073/pnas.1323533111

Manrique, H. M., & Call, J. (2015). Age-dependent cognitive inflexibility in great apes. Animal *Behaviour, 102,* 1–6. https://doi.org/10.1016/j.anbehav.2015.01.002

Manrique, H. M., Völter, C. J., & Call, J. (2013). Repeated innovation in great apes. *Animal Behaviour, 85*(1), 195–202. https://doi.org/10.1016/j.anbehav.2012.10.026

Marcovitch, S., & Zelazo, P. D. (1999). The A-Not-B Error: Results from a Logistic Meta-Analysis. *Child Development*, *70*(6), 1297–1313. https://doi.org/10.1111/1467-8624.00095

Marcovitch, S., & Zelazo, P. D. (2006). The influence of number of A trials on 2-year-olds' behavior in two A-not-B type search tasks: A test of the hierarchical competing systems model. Journal of Cognition and Development, 7(4), 477-501. DOI: 10.1207/s15327647jcd0704_3

Marcovitch, S., & Zelazo, P. D. (2009). A hierarchical competing systems model of the emergence and early development of executive function. *Developmental Science*, *12*(1), 1–25. https://doi.org/10.1111/j.1467-7687.2008.00754.x

Margolis, E., Laurence, S., & Barrett, H. C. (2008). Artifacts and Original Intent: A Cross-Cultural Perspective on the Design Stance. *Journal of Cognition and Culture, 8*(1), 1–22. https://doi.org/10.1163/156770908X289189

Marsh, H. L., & Legerstee, M. (2016). Awareness of goal-oriented behavior during infancy and early childhood, in human- and non-human primates. *Infant Behavior and Development*, (April 2015), 1–8. https://doi.org/10.1016/j.infbeh.2016.11.010

Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (Pan troglodytes) and the question of cumulative culture: an experimental approach. *Animal Cognition*, *11*(3), 449–56. https://doi.org/10.1007/s10071-007-0135-y

Martin-Ordas, G., Haun, D., Colmenares, F., & Call, J. (2010). Keeping track of time: evidence for episodic-like memory in great apes. *Animal Cognition*, *13*(2), 331–40. https://doi.org/10.1007/s10071-009-0282-4

Marton, K., Kelmenson, L., & Pinkhasova, M. (2008). Inhibition control and working memory capacity in children with SLI. *Psychologia (Ramat-Gan), 50*(2), 110–121.

Mason, W. a, Jones, A., & Goldstone, R. L. (2008). Propagation of innovations in networked groups. *Journal of Experimental Psychology. General*, *137*(3), 422–433. https://doi.org/10.1037/a0012798

Mason, W., & Watts, D. J. (2012). Collaborative learning in networks. *Proceedings of the National Academy of Sciences*, *109*(3), 764–769. https://doi.org/10.1073/pnas.1110069108/-/DCSupplemental.www.pnas.org/cgi/doi/10.1073/pnas.1110069108

McElreath, R. (2015). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. Chapman & Hall, CRC Press.

McGuigan, N., Gladstone, D., & Cook, L. (2012). Is the cultural transmission of irrelevant tool actions in adult humans (*Homo sapiens*) best explained as the result of an evolved conformist bias? *PloS One*, *7*(12), e50863. https://doi.org/10.1371/journal.pone.0050863

McGuigan, N., Makinson, J., & Whiten, A. (2011). From over-imitation to super-copying: adults imitate causally irrelevant aspects of tool use with higher fidelity than young children. *British Journal of Psychology (London, England : 1953)*, *102*(1), 1–18.

https://doi.org/10.1348/000712610X493115

McGuigan, N., & Whiten, A. (2009). Emulation and "overemulation" in the social learning of causally opaque versus causally transparent tool use by 23- and 30-month-olds. *Journal of Experimental Child Psychology*, *104*(4), 367–81. https://doi.org/10.1016/j.jecp.2009.07.001

McNab, F., Leroux, G., Strand, F., Thorell, L., Bergman, S., & Klingberg, T. (2008). Common and unique components of inhibition and working memory: An fMRI, within-subjects investigation. *Neuropsychologia*, *46*(11), 2668–2682. https://doi.org/10.1016/j.neuropsychologia.2008.04.023

McPherron, S. P., Alemseged, Z., Marean, C. W., Wynn, J. G., Reed, D., Geraads, D., ... Béarat, H. a. (2010). Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature*, *466*(7308), 857–60. https://doi.org/10.1038/nature09248

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., & Boesch, C. (2007). 4,300-Year-old chimpanzee sites and the origins of percussive stone technology. *Proceedings of the National Academy of Sciences, 104*(9), 3043–3048. https://doi.org/10.1073/pnas.0607909104

Mesoudi, A. (2008). An experimental simulation of the "copy-successful-individuals" cultural learning strategy: adaptive landscapes, producer–scrounger dynamics, and informational access costs. *Evolution and Human Behavior*, *29*(5), 350–363. https://doi.org/10.1016/j.evolhumbehav.2008.04.005

Mesoudi, A. (2011a). An experimental comparison of human social learning strategies: payoff-biased social learning is adaptive but underused. *Evolution and Human Behavior*, *32*(5), 334–342. https://doi.org/10.1016/j.evolhumbehav.2010.12.001

Mesoudi, A. (2011b). Variable Cultural Acquisition Costs Constrain Cumulative Cultural Evolution. *PloS One*, *6*(3), e18239. https://doi.org/10.1371/journal.-pone.0018239

Mesoudi, A. (2015). Cultural Evolution: Integrating Psychology, Evolution and Culture. *Current Opinion in Psychology*, *7*, 17–22. https://doi.org/10.1016/j.copsyc.2015.07.001

Mesoudi, A., & Brien, M. J. O. (2008). The cultural transmission of great basin projectile-

point technology i : an experimental simulation, *American Antiquity*, *73*(1), 3–28.

Miller, E. K. (2000). The prefrontal cortex and cognitive control. *Nature Reviews Neuroscience, 1*(October), 13–15.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of cognitive control. *Annual Review of Neuroscience*, *24*, 167–202.

Miyake, A., & Friedman, N. P. (2012). The Nature and Organisation of Individual Differences in Executive Functions : Four General Conclusions. *Current Directions in Psychological Science, 21*(1), 8–14. https://doi.org/10.1177/0963721411429458.The

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, a H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex "Frontal Lobe" tasks: a latent variable analysis. *Cognitive Psychology, 41*(1), 49–100. https://doi.org/10.1006/cogp.1999.0734

Moll, H., & Tomasello, M. (2007). Cooperation and human cognition: the Vygotskian intelligence hypothesis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1480), 639–48. https://doi.org/10.1098/rstb.2006.2000

Mölle, M., Marshall, L., Wolf, B., Fehm, H. L., & Born, J. (1999). EEG complexity and performance measures of creative thinking. *Psychophysiology, 36*(1), S0048577299961619. https://doi.org/10.1017/S0048577299961619

Montague, P. R., King-Casas, B., & Cohen, J. D. (2006). Imaging Valuation Models in Human Choice. *Annual Review of Neuroscience*, *29*(1), 417–448. https://doi.org/10.1146/annurev.neuro.29.051605.112903

Morgan, T. J. H., Rendell, L. E., Ehn, M., Hoppitt, W., & Laland, K. N. (2012). The evolutionary basis of human social learning. *Proceedings. Biological Sciences / The Royal Society*, *279*(1729), 653–62. https://doi.org/10.1098/rspb.2011.1172

Morgan, T. J. H., Uomini, N. T., Rendell, L. E., Chouinard-Thuly, L., Street, S. E., Lewis, H. M., ... Laland, K. N. (2015). Experimental evidence for the co-evolution of hominin tool-making teaching and language. *Nature Communications*, *6*, 6029. https://doi.org/10.1038/ncomms7029

Morin, O. (2016). *How traditions live and die.* Oxford: Oxford University Press

Morton, J. B., & Munakata, Y. (2002). Active versus latent representations: A neural network model of perseveration, dissociation, and decalage. *Developmental Psychobiology*, *40*(3), 255–265. https://doi.org/10.1002/dev.10033

Mostofsky, S. H., Schafer, J. G. B., Abrams, M. T., Goldberg, M. C., Flower, A. A., Boyce, A., ... Pekar, J. J. (2003). f MRI evidence that the neural basis of response inhibition is task-dependent. *Cognitive Brain Research, 17,* 419–430. https://doi.org/10.1016/S0926-6410(03)00144-7

Munakata, Y. (2001). Graded representations in behavioral dissociations. *Trends in Cognitive Science, 5*(7), 309–315.

Munakata, Y., Herd, S., Chatham, C., Depue, B. E., Banich, M. T., & O'Reilly, R. C. (2011). A unified framework for inhibitory control. *Trends in Cognitive Sciences, 15*(10), 453–459. https://doi.org/10.1016/j.tics.2011.07.011.A

Munakata, Y., Snyder, H. R., & Chatham, C. H. (2012). Developing Cognitive Control: Three Key Transitions. *Current Directions in Psychological Science*, *21*(2), 71–77. https://doi.org/10.1016/j.immuni.2010.12.017.Two-stage

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports*, *6*(October), 34783. https://doi.org/10.1038/srep34783

Muthukrishna, M., Shulman, B. W., Vasilescu, V., & Henrich, J. (2014). Sociality influences cultural complexity. *Proceedings. Biological Sciences / The Royal Society*, *281*(1774), 20132511. https://doi.org/10.1098/rspb.2013.2511

Nakahashi, W. (2007). The evolution of conformist transmission in social learning when the environment changes periodically. *Theoretical Population Biology*, *72*(1), 52–66. https://doi.org/10.1016/j.tpb.2007.03.003

Nakahashi, W., Wakano, J. Y., & Henrich, J. (2012). Adaptive social learning strategies in temporally and spatially varying environments : how temporal vs. spatial variation, number of cultural traits, and costs of learning influence the evolution of conformist-biased transmission, payoff-biased transmissi. *Human Nature (Hawthorne, N.Y.)*, *23*(4), 386–418. https://doi.org/10.1007/s12110-012-9151-y

Nedic, B. A., Tomlin, D., Holmes, P., Prentice, D. A., & Cohen, J. D. (2012). A Decision Task in a Social Context : Human Experiments , Models , and Analyses of Behavioral Data. *Proceedings of the IEEE*, *100*(3), 713–733.

Nehaniv, C. L., & Dautenhahn, K. (2002). The correspondence problem In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts*. Cambridge, MA: MIT Press.

Nielsen, M., & Tomaselli, K. (2010). Overimitation in Kalahari Bushman children and the origins of human cultural cognition. *Psychological Science*, *21*(5), 729–36. https://doi.org/10.1177/0956797610368808

Nigg, J. T. (2000). On inhibition/disinhibition in developmental psychopathology: Views from cognitive and personality psychology and a working inhibition taxonomy. *Psychological Bulletin, 126*, 220–246.

Nishida, T., Matsusaka, T., & McGrew, W. C. (2009). Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates; Journal of Primatology*, *50*(1), 23–36. https://doi.org/10.1007/s10329-008-0109-y

O'Doherty, J. P., Cockburn, J., & Pauli, W. M. (2017). Learning, Reward, and Decision Making. *Annual Review of Psychology*, *68*(1), annurev-psych-010416-044216. https://doi.org/10.1146/annurev-psych-010416-044216

Osvath, M., Kabadayi, C., & Jacobs, I. (2014). Independent Evolution of Similar Complex Cognitive Skills: The Importance of Embodied Degrees of Freedom. *Animal Behavior and Cognition*, *1*(3), 249. https://doi.org/10.12966/abc.08.03.2014

Osvath, M., & Osvath, H. (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Animal Cognition*, *11*(4), 661–674. https://doi.org/10.1007/s10071-008-0157-0

Padmala, S., & Pessoa, L. (2010). Interactions between cognition and motivation during response inhibition. *Neuropsychologia, 48*(2), 558–565. https://doi.org/10.1016/j.neuropsychologia.2009.10.017

Piaget, J. (1954) The construction of reality in the child. Basic Books, New York. Pope, S. M., Meguerditchian, A., Hopkins, W. D., & Fagot, J. (2015). Baboons (*Papio papio*), but not

humans, break cognitive set in a visuomotor task. *Animal Cognition, 18*(6), 1339–1346. https://doi.org/10.1007/s10071-015-0904-y

Pope, S. M., Meguerditchian, A., Hopkins, W. D., & Fagot, J. (2015). Baboons (*Papio papio*), but not humans, break cognitive set in a visuomotor task. *Animal Cognition*, *18*(6), 1339–1346. doi:10.1007/s10071-015-0904-y

Powell, A., Shennan, S., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, *324*(5932), 1298–301. https://doi.org/10.1126/science.1170165

Pradhan, G. R., Tennie, C., & van Schaik, C. P. (2012). Social organization and the evolution of cumulative technology in apes and hominins. *Journal of Human Evolution*, *63*(1), 180–90. https://doi.org/10.1016/j.jhevol.2012.04.008

Price, E. E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. Proceedings. *Biological Sciences / The Royal Society, 276*(1671), 3377–83. https://doi.org/10.1098/rspb.2009.0640

Price, E. E., Wood, L. A., & Whiten, A. (2016). Adaptive cultural transmission biases in children and nonhuman primates. *Infant Behavior and Development*. https://doi.org/10.1016/j.infbeh.2016.11.003

Pushina, N. N., Orekhova, E. V., & Stroganova, T. A. (2005). Age-related and individual differences in the performance of a delayed response task (the A-not-B task) in infant twins aged 7-12 months. *Neuroscience and Behavioral Physiology*, *35*(5), 481–490. https://doi.org/10.1007/s11055-005-0083-4

Reader, S. M., & Biro, D. (2010). Experimental identification of social learning in wild animals. *Learning & Behavior*, *38*(3), 265–83. https://doi.org/10.3758/LB.38.3.265

Reader, S. M., & Laland, K. N. (2001). Primate Innovation : Sex , Age and Social Rank Differences. *International Journal of Primatology*, *22*(5), 787–805.

Redick, T. S., Calvo, A., Gay, C. E., & Engle, R. W. (2011). Working memory capacity and go/no-go task performance: selective effects of updating, maintenance, and inhibition. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 37*(2), 308–324. https://doi.org/10.1037/a0022216

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M. W., ... Laland, K.

N. (2010). Why copy others? Insights from the social learning strategies tournament. *Science*, *328*(5975), 208–213. https://doi.org/10.1126/science.1184719

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, *15*(2), 68–76. https://doi.org/10.1016/j.tics.2010.12.002

Reverberi, C., Toraldo, A., D'Agostini, S., & Skrap, M. (2005). Better without (lateral) frontal cortex? Insight problems solved by frontal patients. *Brain, 128*(12), 2882–2890. https://doi.org/10.1093/brain/awh577

Reynolds, J. R., O'Reilly, R. C., Cohen, J. D., & Braver, T. S. (2012). The function and organization of lateral prefrontal cortex: A test of competing hypotheses. *PLoS ONE*, *7*(2). https://doi.org/10.1371/journal.pone.0030284

Richerson, P., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

Rieucau, G., & Giraldeau, L.-A. (2011). Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 949–957. https://doi.org/10.1098/rstb.2010.0325

Roberts, R. J., Hager, L. D., & Heron, C. (1994). Prefrental Cognitive Processes : Working Memory and Inhibition in the Antisaccade Task. *Journal of Experimental Psychology, 123*(4), 374–393.

Roberts, R. J., & Pennington, B. F. (1996). An interactive framework for examining prefrontal cognitive processes. *Developmental Neuropsychology, 12*(1), 105–126.

Rogers, A. R. (1988). Does Biology Constrain Culture. *American Anthropologist*, *90*(4), 819–831. https://doi.org/10.1525/aa.1988.90.4.02a00030

Romberg, A. R., & Saffran, J. R. (2010). Statistical learning and language acquisition. Wiley Interdisciplinary Reviews: *Cognitive Science, 1*(6), 906–914. https://doi.org/10.1002/wcs.78

Rushworth, M. F. S., Kolling, N., Sallet, J., & Mars, R. B. (2012). Valuation and decision-making in frontal cortex: One or many serial or parallel systems? *Current Opinion in*

Neurobiology, *22*(6), 946–955. https://doi.org/10.1016/j.conb.2012.04.011

Sanz, C., Call, J., & Morgan, D. (2009). Design complexity in termite-fishing tools of chimpanzees (Pan troglodytes). *Biology Letters*, *5*(3), 293–6. https://doi.org/10.1098/rsbl.2008.0786

Sanz, C. M., Schöning, C., & Morgan, D. B. (2010). Chimpanzees prey on army ants with specialized tool set. *American Journal of Primatology*, *72*(1), 17–24. https://doi.org/10.1002/ajp.20744

Schlag, K. H. (1998). Why Imitate, and If So, How? *Journal of Economic Theory*, *78*(1), 130–156. https://doi.org/10.1006/jeth.1997.2347

Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology. Animal Behavior Processes, 35*(1), 23–34. https://doi.org/10.1037/a0012925

Seed, A., Seddon, E., Greene, B., & Call, J. (2012). Chimpanzee "folk physics": bringing failures into focus. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 367*(1603), 2743–52. https://doi.org/10.1098/rstb.2012.0222

Selman, B., Kautz, H. A., & Cohen, B. (1994). Noise strategies for improving local search. *Association for the Advancement of Artificial Intelligence*, 337–343.

Semaw, S., Rogers, M. J., Quade, J., Renne, P. R., Butler, R. F., Dominguez-Rodrigo, M., ... Simpson, S. W. (2003). 2.6-Million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution*, *45*(2), 169–177. https://doi.org/10.1016/S0047-2484(03)00093-9

Siegler, R. S. (1996). *Emerging minds: The process of change in children's thinking*. New Youk: Oxford University Press.

Simmonds, D. J., Pekar, J. J., & Mostofsky, S. H. (2008). Meta-analysis of Go/No-go tasks demonstrating that fMRI activation associated with response inhibition is task-dependent. *Neuropsychologia*, *46*(1), 224–232. https://doi.org/10.1016/j.neuropsychologia.2007.07.015

Sirianni, G., Mundry, R., & Boesch, C. (2015). When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Animal*

Behaviour, *100*, 152–165. https://doi.org/10.1016/j.anbehav.2014.11.022

Smith, K. S., & Graybiel, A. M. (2014). Investigating habits: strategies, technologies and models. *Frontiers in Behavioral Neuroscience*, *8*(February), 39. https://doi.org/10.3389/fnbeh.2014.00039

Smith, K. S., & Graybiel, A. M. (2016). Habit formation. *Dialogues in Clinical Neuroscience*, *18*(4), 33–43.

Stedron, J. M., Sahni, S. D., & Munakata, Y. (2005). Common Mechanisms for Working Memory and Attention : The Case of Perseveration with Visible Solutions. *Journal of Cognitive Neuroscience, 17*(4), 623–631.

Stokes, E., & Byrne, R. (2001). Cognitive capacities for behavioural flexibility in wild chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food processing. *Animal Cognition*, *4*(1), 11–28. https://doi.org/10.1007/s100710100082

Stout, D. (2011). Stone toolmaking and the evolution of human culture and cognition. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1050–9. https://doi.org/10.1098/rstb.2010.0369

Strimling, P., Enquist, M., & Eriksson, K. (2009). Repeated learning makes cultural evolution unique. *Proceedings of the National Academy of Sciences*, *106*(33), 13870–13874.

Subiaul, F., & Schilder, B. (2014). Working memory constraints on imitation and emulation. *Journal of Experimental Child Psychology*, *128*, 190–200. https://doi.org/10.1016/j.jecp.2014.07.005

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1528), 2405–15. https://doi.org/10.1098/rstb.2009.0052

Tennie, C., Call, J., & Tomasello, M. (2010). Evidence for emulation in chimpanzees in social settings using the floating peanut task. *PloS One*, *5*(5), e10544. https://doi.org/10.1371/journal.pone.0010544

Tennie, C., Call, J., & Tomasello, M. (2012). Untrained chimpanzees (*Pan troglodytes schweinfurthii*) fail to imitate novel actions. *PloS One*, *7*(8), e41548. https://doi.org/10.1371/journal.pone.0041548

Theeuwes, J. (2010). Top–down and bottom–up control of visual selection. *Acta Psychologica, 135*(2), 77–99. https://doi.org/10.1016/j.actpsy.2010.02.006

Thelen, E., Schöner, G., Scheier, C., & Smith, L. B. (2001). The dynamics of embodiment : A field theory of infant perseverative reaching, *Behavioral Brain Science, 24*(1), 1–86.

Thompson-schill, S. L., Ramscar, M., & Chrysikou, E. G. (2009). Cognition without control- When a Little Frontal Lobe Goes a Long Way. *Psychological Science, 18*(5), 259–263. https://doi.org/10.1111/j.1467-8721.2009.01648.x

Thorndike, E. L. (1898). Animal intelligence: an experimental study of the associative processes in animals. *Psychological Review Monograph Supplement, 2*(4):1–109

Thornton, A. & McAuliffe, K (2006). Teaching in Wild Meerkats. *Science, 313*(5784), 227–229.

Toelch, U., Bruce, M. J., Meeus, M. T. H., & Reader, S. M. (2011). Social performance cues induce behavioral flexibility in humans. *Frontiers in Psychology, 2*(JUL), 160. https://doi.org/10.3389/fpsyg.2011.00160

Tomasello, M. (2016). Cultural Learning Redux. *Child Development, 87*(3), 643–653. https://doi.org/10.1111/cdev.12499

Tomasello, M., & Call, J. (2004). The role of humans in the cognitive development of apes revisited. *Animal Cognition, 7*(4), 213–215. https://doi.org/10.1007/s10071-004-0227-x

Tomasello, M., Carpenter, M. & Hobson, R. P. (2003). The emergence of social cognition in three young chimpanzees. *Monog. Soc. Res. Child Dev.* 70, i+vii+1–152

Tomasello, M., Kruger, A.C., & Ratner, H.H. (1993). Cultural learning. *Behavioral and Brian Sciences, 16,* 495-552.

Tomasello, M., Melis, A. P., Tennie, C., Wyman, E., & Herrmann, E. (2012). Two Key Steps in the Evolution of Human Cooperation. *Current Anthropology, 53*(6), 673–692. https://doi.org/10.1086/668207

Tomlin, D., Nedic, A., Prentice, D. A., Holmes, P., & Cohen, J. D. (2013). The Neural Substrates of Social Influence on Decision Making. *PLoS ONE, 8*(1). https://doi.org/10.1371/journal.pone.0052630

Tooby, J., & DeVore, I. (1987). The reconstruction of hominid behavioural evolution through strategic modelling. In W.G. Kinsey (Eds.) *The Evolution of Human Behaviour: Primate Models* (183-237). Albany, NY: SUNY Press

Topal, J., Gergely, G., Miklosi, a., Erdohegyi, a., & Csibra, G. (2008). Infants' Perseverative Search Errors Are Induced by Pragmatic Misinterpretation. *Science*, *321*(5897), 1831–1834. https://doi.org/10.1126/science.1161437

Toth, N., Schick, K. D., Savage-Rumbaugh, E. S., Sevcik, R. A., & Rumbaugh, D. M. (1993) Pan the tool-maker: investigations into the stone tool-making and tool- using capabilities of a bonobo (*Pan paniscus*). *Journal of Archaeological Science, 20*(1), 81–91. (doi:10.1006/jasc. 1993.1006)

Tricomi, E. M., Balleine, B. W., & O'Doherty, J. P. (2009). A specific role for posterior dorsolateral striatum in human habit learning. *The European Journal of Neuroscience*, *29*(11), 2225–2232. https://doi.org/10.1111/j.1460-9568.2009.06796.x.A

Vaesen, K. (2012). Cumulative cultural evolution and demography. *PloS One*, *7*(7), e40989. https://doi.org/10.1371/journal.pone.0040989

Vale, G. L., Davis, S. J., van de Waal, E., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2017). Lack of conformity to new local dietary preferences in migrating captive chimpanzees. *Animal Behaviour*, *124*, 135–144. https://doi.org/10.1016/j.anbehav.2016.12.007

Vale, G.L., Flynn, E.G., Hopper, L.M., Lambeth, S.P., Schapiro, S.J., & Kendal, R.L. (in prep). Payoff Biased Copying in Chimpanzees (*Pan troglodytes*) and Children (H*omo sapiens*) in Vale, G. L. (2013). *Investigating success biased transmission, and long-term memory capabilities, in chimpanzees and children: implications for cumulative culture* (Doctoral dissertation). Durham University, United Kingdom.

Vale, G. L., Flynn, E. G., Pender, L., Price, E., Whiten, A., Lambeth, S. P., ...Kendal, R. L. (2016). Robust retention and transfer of tool construction techniques in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 130*(1), 24–35. https://doi.org/10.1037/a0040000

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, *340*(6131), 483–5. https://doi.org/10.1126/science.1232769

van der Post, D. J., Franz, M., & Laland, K. N. (2017). The evolution of social learning mechanisms and cultural phenomena in group foragers. *BMC Evolutionary Biology*, *17*(1), 49. https://doi.org/10.1186/s12862-017-0889-z

van Leeuwen, E. J. C., & Call, J. (2016). Conservatism and "copy-if-better" in chimpanzees (*Pan troglodytes*). *Animal Cognition*. https://doi.org/10.1007/s10071-016-1061-7

van Leeuwen, E. J. C., Call, J., & Haun, D. B. M. (2014). Human children rely more on social information than chimpanzees do Human children rely more on social information than chimpanzees do, (November).

van Leeuwen, E. J. C., Cronin, K. a, & Haun, D. B. M. (2014). A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*). *Animal Cognition*, *17*(6), 1421–5. https://doi.org/10.1007/s10071-014-0766-8

Van Leeuwen, E. J. C., Cronin, K. a, Schütte, S., Call, J., & Haun, D. B. M. (2013). Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PloS One*, *8*(11), e80945. https://doi.org/10.1371/journal.pone.0080945

van Leeuwen, E. J. C., & Haun, D. B. M. (2013). Conformity in nonhuman primates: fad or fact? *Evolution and Human Behavior*, *34*(1), 1–7. https://doi.org/10.1016/j.evolhumbehav.2012.07.005

van Schaik, C. P. (2012). Animal culture: chimpanzee conformity? *Current Biology : CB*, *22*(10), R402-4. https://doi.org/10.1016/j.cub.2012.04.001

van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 1008–16. https://doi.org/10.1098/rstb.2010.0304

Vlamings, P. H. J. M., Hare, B., & Call, J. (2009). Reaching around barriers: the performance of the great apes and 3–5-year-old children. *Animal Cognition, 13*(2), 273–285. https://doi.org/10.1007/s10071-009-0265-5

Völter, C. J., & Call, J. (2012). Problem solving in great apes (*Pan paniscus, Pan troglodytes, Gorilla gorilla,* and *Pongo abelii*): the effect of visual feedback. *Animal Cognition, 15*(5), 923–36. https://doi.org/10.1007/s10071-012-0519-5

Washburn, D. A. (2016). The Stroop effect at 80: The competition between stimulus control and cognitive control. *Journal of the Experimental Analysis of Behavior*, *105*(1), 3–13. https://doi.org/10.1002/jeab.194

Watanabe, H., Forssman, L., Green, D., Bohlin, G., & von Hofsten, C. (2012). Attention demands influence 10- and 12-month-old infants' perseverative behavior. *Developmental Psychology*, *48*(1), 46–55. https://doi.org/10.1037/a0025412

Wasielewski, H. (2014). Imitation is necessary for cumulative cultural evolution in an unfamiliar, opaque task. *Human Nature (Hawthorne, N.Y.)*, *25*(1), 161–79. https://doi.org/10.1007/s12110-014-9192-5

Whalen, A., Cownden, D., & Laland, K. (2015). The learning of action sequences through social transmission. *Animal Cognition*, *18*(5), 1093–103. https://doi.org/10.1007/s10071-015-0877-x

Whiten, A. (1999a). The evolution of deep social mind in humans. In S.E.G. Lea and M.C. Corballis (Eds.), *The Descent of Mind*. Oxford: Oxford University Press.

Whiten, A. (1999b). Parental encouragement in *Gorilla* in comparative perspective: Implications for social cognition and the evolution of teaching in S.T. Parker, R.W. Mitchell and H.L. Miles (Eds.) *The Mentalities of Gorillas and Orangutans: Comparative Perspectives*. Cambridge, UK: Cambridge University Press.

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature*, *437*(7055), 52–5. https://doi.org/10.1038/nature04023

Whiten, A. (2011). The scope of culture in chimpanzees, humans and ancestral apes. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1567), 997–1007. https://doi.org/10.1098/rstb.2010.0334

Whiten, A. (2015). Experimental studies illuminate the cultural transmission of percussive technologies in Homo and Pan. *Philosophical Transactions of the Royal Society of London. B*, *370*(20140359), 1–13. https://doi.org/10.1098/rstb.2014.0359

Whiten, A. (2017). Social Learning and Culture in Child and Chimpanzee. *Annual Review of Neuroscience*, *68*, 129–154. https://doi.org/10.1146/annurev-psych-010416-044108

Whiten, A., Caldwell, C. A., & Mesoudi, A. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology, 8,* 15–21. https://doi.org/10.1016/j.copsyc.2015.09.002

Whiten, A., & Erdal, D. (2012). The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1599), 2119–2129. https://doi.org/10.1098/rstb.2012.0114

Whiten, A., & Flynn, E. (2010). The transmission and evolution of experimental microcultures in groups of young children. *Developmental Psychology, 46*(6), 1694–709. https://doi.org/10.1037/a0020786

Whiten, A., Goodall, J., Mcgrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., ... Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*, 682–685.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*(7059), 737–40. https://doi.org/10.1038/nature04047

Whiten, A., Horner, V., Litchfield, C. a., & Marshall-Pescini, S. (2004). How do apes ape? *Animal Learning & Behavior*, *32*(1), 36–52. https://doi.org/10.3758/BF03196005

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1528), 2417–28. https://doi.org/10.1098/rstb.2009.0069

Whiten, A., & Mesoudi, A. (2008). Review. Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 363*(1509), 3477–88. https://doi.org/10.1098/rstb.2008.0134

Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J., & de Waal, F. B. M. (2007). Transmission of multiple traditions within and between chimpanzee groups. *Current Biology : CB*, *17*(12), 1038–43. https://doi.org/10.1016/j.cub.2007.05.031

Whiten, A., & van Schaik, C. P. (2007). The evolution of animal "cultures" and social intelligence. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1480), 603–20. https://doi.org/10.1098/rstb.2006.1998

Whiten, A., & van de Waal, E. (2016). Social learning, culture and the "socio-cultural brain" of human and non-human primates. *Neuroscience & Biobehavioral Reviews*. https://doi.org/10.1016/j.neubiorev.2016.12.018

Wiley, J. (1998). Expertise as mental set : The effects of domain knowledge in creative problem solving. *Memory & Cognition, 26*(4), 716–730.

Wilfried, E. E. G., & Yamagiwa, J. (2014). Use of tool sets by chimpanzees for multiple purposes in Moukalaba-Doudou National Park, Gabon. *Primates*, *55*(4), 467–472. https://doi.org/10.1007/s10329-014-0431-5

Wobber, V., Herrmann, E., Hare, B., Wrangham, R., & Tomasello, M. (2014). Differences in the early cognitive development of children and great apes. *Developmental Psychobiology*, *56*(3), 547–73. https://doi.org/10.1002/dev.21125

Wood, L. A., Kendal, R. L., & Flynn, E. G. (2012). Context-dependent model-based biases in cultural transmission: children's imitation is affected by model age over model knowledge state. *Evolution and Human Behavior*, *33*(4), 387–394. https://doi.org/10.1016/j.evolhumbehav.2011.11.010

Wood, L. A, Kendal, R. L., & Flynn, E. G. (2013). Copy me or copy you? The effect of prior experience on social learning. *Cognition, 127*(2), 203–13. https://doi.org/10.1016/j.cognition.2013.01.002

Yamamoto, S., Humle, T., & Tanaka, M. (2013). Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PloS One, 8*(1), e55768. https://doi.org/10.1371/journal.pone.0055768

Yamamoto, S., Yamakoshi, G., Humle, T., & Matsuzawa, T. (2008). Invention and modification of a new tool use behavior: ant-fishing in trees by a wild chimpanzee (Pan troglodytes verus) at Bossou, Guinea. *American Journal of Primatology*, *70*(7), 699–702. https://doi.org/10.1002/ajp.20544

Youn, H., Strumsky, D., Luis, M. A., Bettencourt, L. M. A., & Lobo, J. (2015). Invention as a combinatorial process: Evidence from U.S. Patents. *Journal of the Royal Society Interface, 12*(106), https://doi.org/10.1098/rsif.2015.0272

Zelazo, P. D. (2006). The Dimensional Change Card Sort (DCCS): a method of assessing executive function in children. *Nature Protocols, 1*(1), 297–301. https://doi.org/10.1038/nprot.2006.46

Zelazo, P. D., Müller, U., Frye, D., Marcovitch, S., Argitis, G., Boseovski, J., ... Sutherland, A. (2003). The development of executive function in early childhood. *Monographs of the Society for Research in Child Development, 68*(3), vii-137.

Zentall, T. R. & Galef, B. G. Jr. (1988). *Social Learning: Psychological and Biological Perspectives*. Hillsdale: Lawrence Erlbaum Associates.

Zwirner, E., & Thornton, A. (2015). Cognitive requirements of cumulative culture: teaching is useful but not essential. *Scientific Reports*, *5*(November 2015), 16781. https://doi.org/10.1038/srep16781

APPENDIX 1: COMPARATIVE SERIALBOX

Behavioural flexibility in children and chimpanzees: Improving solution efficiency through relinquishing and combining witnessed behaviours

Sarah J. Davis, Cristine H. Legare, Jennifer M. Clegg, Rachel E. Watson-Jones, Daniel Ikejimba, Steven J. Schapiro, Susan P. Lambeth, Andrew Whiten (*in prep*)

Phase 1: Acquiring an inefficient solution

- 8 Adult chimpanzees housed at the National Center for Chimpanzee Care
- Children aged 3-5 years

- Participant observes an adult human use an inefficient extraction technique to remove a valuable token from the *Serialbox*
- Participant must perform the inefficient method twice

Phase 2: Relinquishing a working inefficient solution

- Participant watches the same human demonstrator use a more efficient extraction technique
- Both methods reliably result in successful extraction
- Participants are given up to three trials to switch to the more efficient method (High switch score of 7 if switching on first trial, 6 on second, 5 on third trial)
- If the participant continues to use the inefficient method, they witness another demonstration of the inefficient method following each inefficient solution they use (up to three demonstrations total)

Phase 3: Relinquishing an extremely inefficient solution

- Only efficient method a reliable means of extraction
- Token placed in dip inside of apparatus, introducing a partial block to using the inefficient method (switch scores of 4 through 2)
- If no switching, the efficient method is scaffolded (Score of 1)

Coding

7 = switching on phase 2, trial 1

6 = switching on phase 2, trial 2

5 = switching on phase 2, trial 3

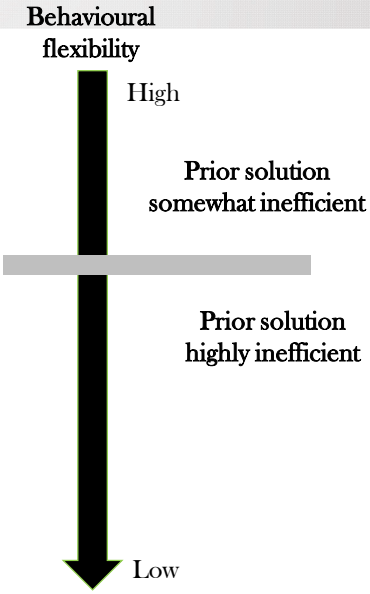
4 = switching on phase 3, trial 1

3 = switching on phase 3, trial 2

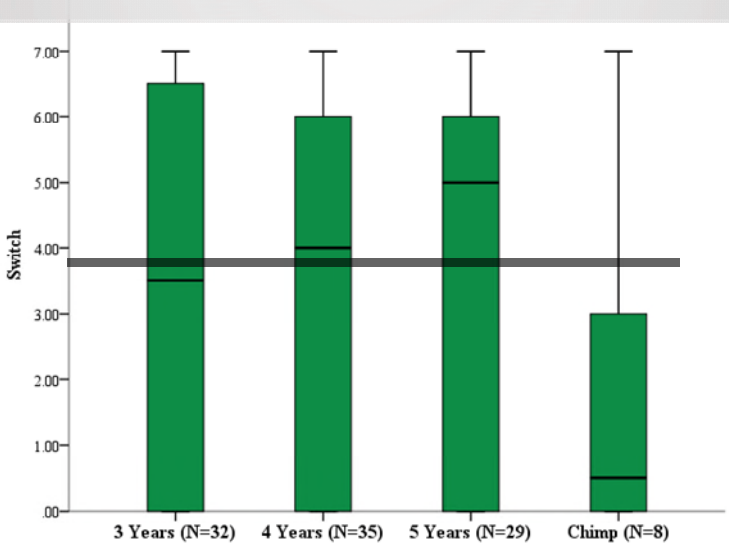
2 = switching on phase 3, trial 3

1 = switching after scaffolding

0 = never having switched



Results



Boxplot showing latency to switch across children aged 3-5 years and chimpanzees. A switch score of 7 indicates an immediate switch to an observed, more efficient method, with lower scores indicating increased latency to switch, and the origin representing no switch to the efficient method. The red bar represents point at which the inefficient method is partially blocked

Behavioural Conservatism in Chimpanzees

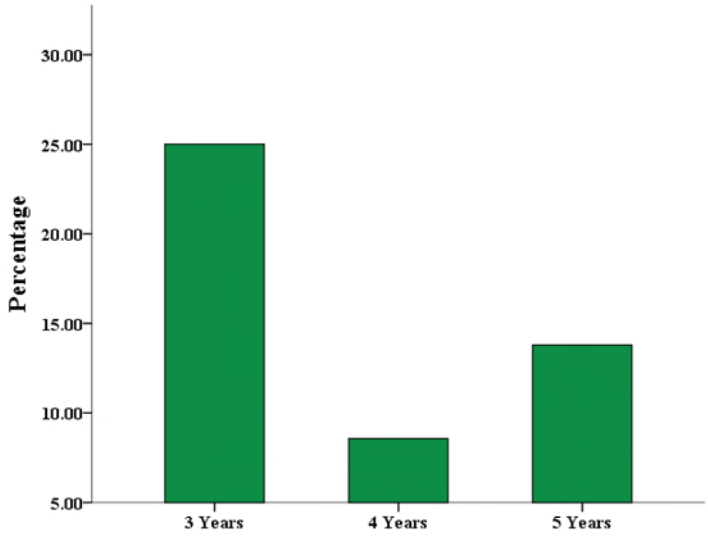
Chimpanzees will perseverate with a complex solution despite potential gains in efficiency, exhibiting difficulties inhibiting this first learned foraging technique to adopt a novel alternative

Results replicate those found in Davis et al., (2016), and are consistent with prior work indicating chimpanzees are behaviourally conservative (Marshall-Pescini & Whiten, 2008; Hrubesh, 2009, Dean et al., 2013)

Perseveration in Children

While there is a lot of variability in the switching behaviours of children, with the median switch scores following predictions generated from increasing cognitive resources, a more subtle interpretation is needed when we consider those who immediately optimise behaviour

Switch on First Trial



Bar chart showing the percentage of participants within their respective age groups who switched immediately after witnessing a demonstration of the more efficient method.

Executive Function

- Preliminary results show that younger children, who at an earlier stage of cognitive development might be expected to perseverate with their prior solution, are often quicker to optimize their behaviour than older children.

- In fact, a quarter of the 29 five year olds so far tested were never seen to switch to the more efficient method, despite repeated failures to successfully solve the task

Indicative that a simple explanatory framework based on availability of cognitive resources may not be adequate to wholly account for suboptimal behaviour in children

Normative Behaviour

These results are not easily explained within a normative framework

- Children see the inefficient solution once but the efficient solution up to 5 times

- We also avoid normative language, using a turn taking procedure

Overall, children do not display strong evidence of imitating the efficient solution

- Less than 15% of children adopting this method after they first witness it

- Even for those who do adopt the efficient solution relatively early in the task, only around 50% faithfully replicate the witnessed action sequence

Additional Behaviours of Interest

Almost 10% of children open the door in phase 3 to remove the block within the apparatus (remove the token from the dip), close the door, and then proceed to use the inefficient method (Insert video below)

APPENDIX 2: A NOT B

BEHAVIOURAL FLEXIBILITY IN CHIMPANZEES (*PAN TROGLODYTES*): INHIBITORY CONTROL IS COMPROMISED FOR WELL-ESTABLISHED BEHAVIOURAL ROUTINES

CONTENTS **PAGE**

PARTICIPANT DEMOGRAPHICS

Table S1 Demographics of participants meeting criterion for inclusion.

Individual	Sex	Age	Wild/captive	Rearing
Al	F	35.45	Captive	Mother
Hd	M	23.62	Captive	Mother
Ty	F	44.64	Wild	Unknown
Ta	F	47.08	Wild	Unknown
Sn	M	31.34	Captive	Mother
Cea	F	24.35	Captive	Mother
Ze	F	13.21	Captive	Mother
Ae	F	40.68	Wild	Unknown
Bte	F	37.56	Captive	Mother
Je	F	25.36	Captive	Mother
Sy	F	44.06	Wild	Unknown
Kt	F	26.96	Captive	Nursery
Ae	F	20.43	Captive	Nursery
Ka	M	35.31	Captive	Mother
Co	F	31.04	Captive	Mother
Jy	M	43.95	Wild	Unknown
Mi	F	25.09	Captive	Mother
Se	F	16.25	Captive	Mother
Na	F	25.12	Captive	Nursery
Gs	M	23.64	Captive	Nursery
Ma	F	49.51	Wild	Unknown
Ci	F	24.69	Captive	Nursery
Hh	F	24.65	Captive	Mother
Pr	F	48.95	Wild	Unknown
Oi	F	31.09	Captive	Mother
Da	F	32.67	Captive	Nursery
Sa	F	25.14	Captive	Mother
Hg	F	17.62	Captive	Mother
Ca	F	34.80	Captive	Mother
Tk	F	35.45	Captive	Mother
Sba	F	47.64	Wild	Unknown
Bn	M	33.91	Captive	Mother
Mo	M	26.92	Captive	Mother
My	M	50.59	Wild	Unknown
Si	M	25.11	Captive	Mother
Ti	M	21.91	Captive	Mother
Ko	M	24.39	Captive	Nursery
Wi	F	33.11	Captive	Mother

From left to right: Individual: Initials of participant; Sex: F = female, M = male; Age: Age in years at time of testing; Captive/wild: Captive = born in captivity, Wild = born in the wild; Rearing: Mother = raised by mother, Nursery = raised by human caretakers.

METHODS

Model construction and choice

Trial type was coded as 0 for A trials or 1 for B trials. Order was coded as 0 (No delay followed by Delay condition) or 1 (Delay followed by No delay condition). No Delay trials were coded as 0 and Delay trials coded as 1. Models were generated through MCMC sampling. Regularising priors were used. As only two outcomes were possible (correct or incorrect reach), GLM models were based on a binomial distribution. Given multiple observations of each participant, partially pooled intercepts where used in some models to account for individual variation in response. Model choice was assessed with reference to Widely Applicable Information Criterion (WAIC), along with posterior predictive checks.

GLMs took the form:

$$1)\ Error \sim Binomial\ (Total\ solutions, p)$$

$$Logit\ (p) < - x$$

With *x* including parameters based on:

i) Order: Does performance decline or improve on the second presentation of task
ii) Delay: Does a delay affect performance
iii) An interaction between order and delay: Does the presence or absence of a delay interact with the order in which the tasks are presented to affect performance
iv) Trial type: Is performance on A trials different from performance on B trials

RESULTS

Performance on B trial

The relationship between predictors and performance on B trial was modelled as

$$1)\ Probability\ of\ error \sim Binomial\ (Total\ solutions, p)$$

$$Logit(p) < -a + Bord * order + bdel * Delay\ +\ bdelord * Delay * order$$

Where *a* is the value of the average intercept, *bord* is the value of the coefficient of the effect of order, *bdel* is the value of the coefficient of the effect of delaying presentation, and *bdelord* is the

value of the coefficient of the interaction between delay and order (Coefficients are summarised in Table S2, along with their 95% credible intervals). Models which did not include a main effect of delay or an interaction effect were given most of the Akaike weight, indicating that delay did not have a credible effect on performance. However, most weight was given to a model including only the main effect of order, with participants doing slightly worse on their second go at the task (median change in probability of error of 0.18, 95% interval of -0.04-0.38; Table S3 and S4; FigureS1 and S2).

Table S2 Coefficients of the model parameters for effect of order and delay on B trials

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-0.91	1.06	-3	1.12
Delay	0.01	1	-1.89	2.01
Order	0.95	0.49	0	1.92
Interaction	-0.33	0.59	-1.44	0.88

Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

Table S3 Model comparison

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
Order	86.5	1.8	0	0.71	2.9	NA
Full	89.4	2	2.9	0.17	4.87	3.94
Main	90.1	2.6	3.5	0.12	4.41	3.4

'Order' is a model including only a main effect of order. 'Full' includes the main effects of order and delay and an interaction between those factors. 'Main' includes only effects of order and delay. WAIC is the Widely Applicable Information Criterion; pWAIC indicates the number of effective parameters; dWAIC is the difference in WAIC values; Weight is the Akaike weight and indicates the effectiveness of the model to describe the data; SE is the standard error of the WAIC estimate; dSE is the standard error of the difference in WAIC of models (McElreath, 2016)

Table S4 Probability of error on first and second presentation of task.

Presentation	Mean	2.5%	97.5%
First	0.41	0.25	0.57
Second	0.59	0.43	0.75

Mean probability of error with 95% credible interval of the probability of error

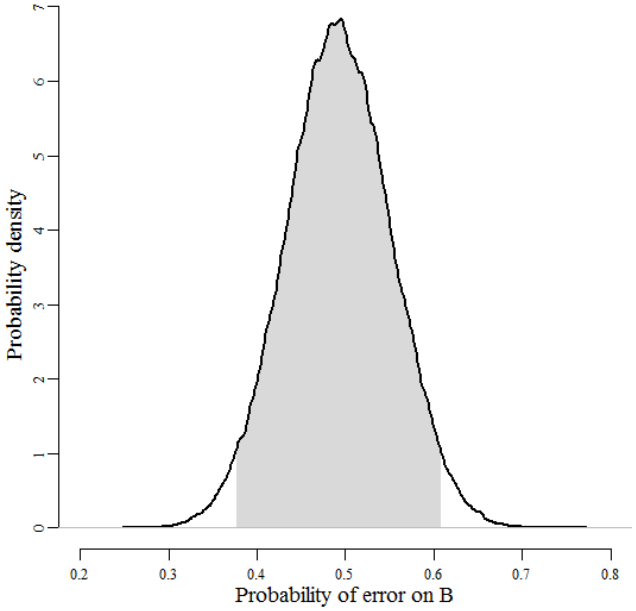


Fig. S1 Posterior distributions of error on all B trials. Light grey shading shows the 95% highest posterior density interval (HPDI)

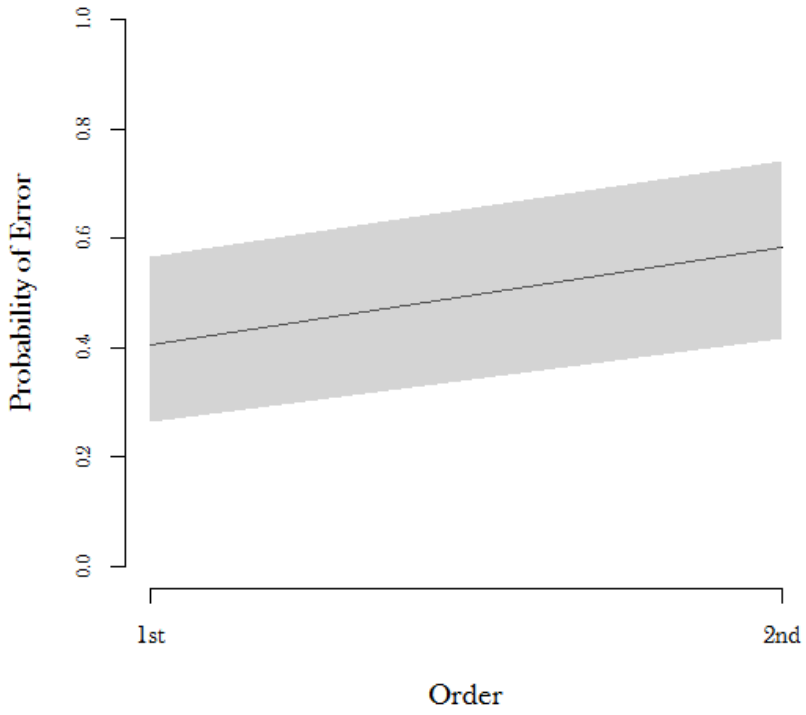


Fig. S2 Effect of Order. Probability of making an error on B trial on 1st and 2nd task presentation. The line represents the mean probability of committing a perseverative error, with the shaded area showing the 95% credible interval of probability of error

Errors on A trials versus B trials

Trial type (A or B) was found to credibly affect the probability of error.

$$Error \sim Binomial\ (Total\ solutions, p)$$

$$Logit(p) < -a + a\_actor[Chimp] + b * Trial\ types$$

Table S5 Coefficients of the model parameters for effect of trial type (A or B)

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-3.09	0.21	-3.49	-2.68
Effect of trial	3.05	0.3	2.48	3.64
Sigma actor	0.92	0.18	0.6	1.27

Table S6 Model predictions for probability of error on A and B trials

Trial type	Median	2.5%	97.5%
A	0.04	0.03	0.06
B	0.49	0.35	0.64

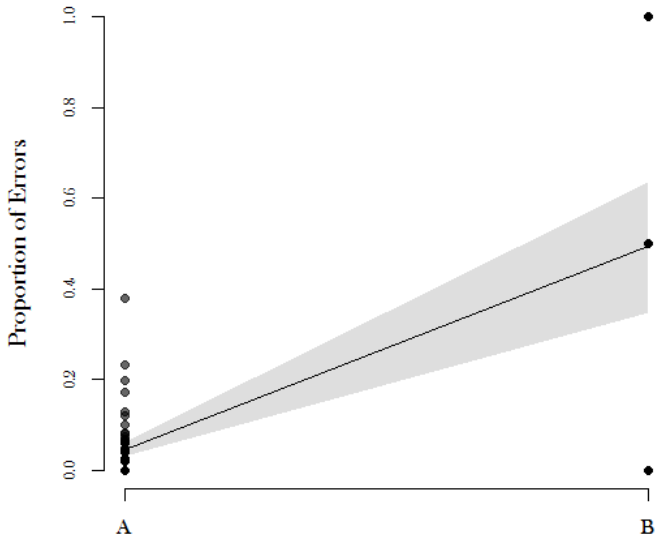


Fig. S3 Model predictions for trial type. Black circles represents the observed proportion of errors made by participants. The black line is the mean expected proportion of reaching errors. The dark grey area is the 95% credible interval

Frequentist analysis

Comparing the proportion of errors made on A trials and B trials A with a within subjects t-test, it was found participants were significantly more likely ($t = -6.7$, $P < .001$) to make an error on B trials (mean =0.47, SD = 0.38) than they were A trials (mean = 0.06, SD = 0.08; Figure S4)

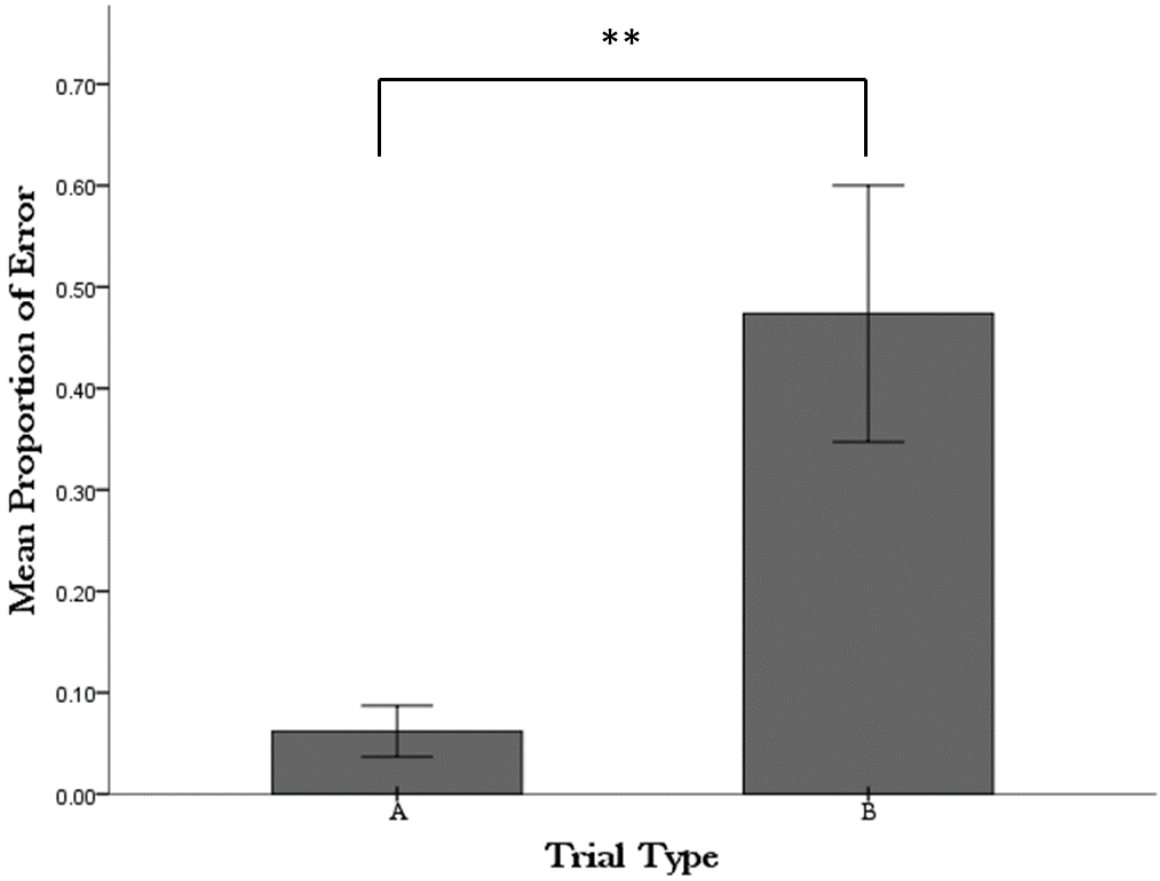


Fig. S4 Mean proportion of errors on A and B trial types. Error bars show the 95% confidence interval

Error on A versus B trials including an order effect

Analyses were conducted on a model of the form

$$Probability\ of\ error \sim Binomial\ (Total\ solutions, p)$$

$$Logit\ (p) \sim a + a_{actor[individual]} + b * Trial\ type + bord * Order + bbord * Trial\ type * Order$$

Including an effect of order and interaction effect better predicted performance than including trial type alone. Model parameters are summarised in Table S7

Table S7 Coefficients of the model parameters for effect of trial type by order

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-2.83	0.21	-3.26	-2.42
Trial type	2.45	0.39	1.7	3.2
Order	-0.63	0.25	-1.11	-0.12
Trial type*Order	0.86	0.17	0.54	1.19

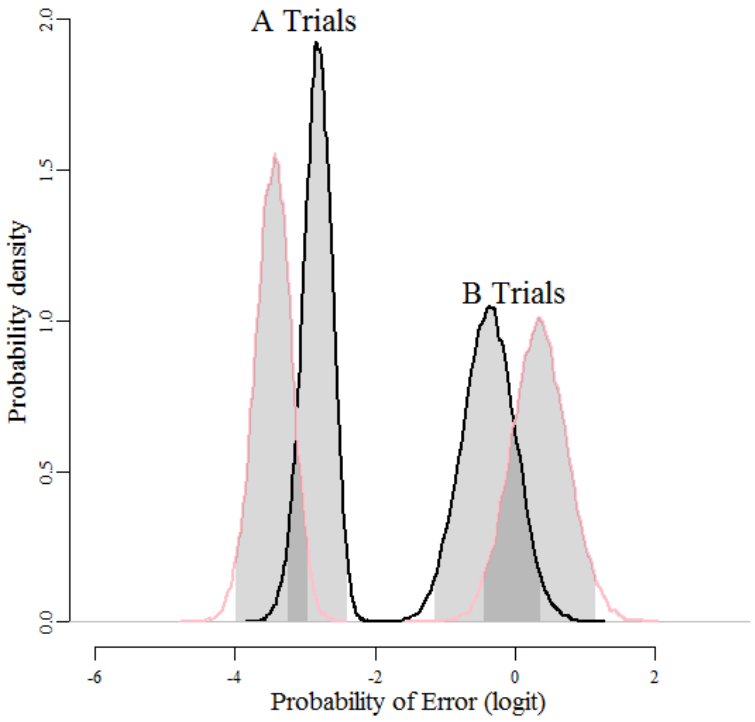


Fig. S5 Posterior distributions for probability of error on A and B trials on 1st and 2nd presentation. Light grey shading shows the 95% highest posterior density interval (HPDI) for each group. Dark grey shading shows the overlap in expected solutions between groups. First presentation data is shown in black and 2nd presentation data is shown in pink

Within task errors on First A trial versus B trial

Looking at performance on the first trial, as modelled by

$$Probability\ of\ error\ on\ 1st\ trial \sim Binomial\ (1, p)$$

$$Logit\ (p) \sim a + a_{actor[individual]} + b * Trial\ type$$

Table S8 Regression predictions for probability of error on first A and B trials

First trial	Median	2.5%	97.5%
A	0.16	0.08	0.25
B	0.49	0.38	0.61

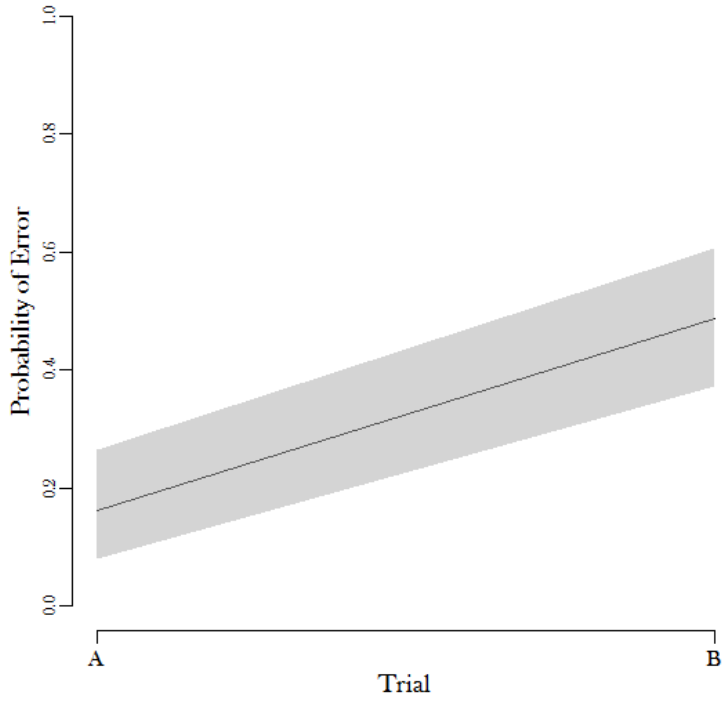


Fig. S6 Regression predictions for first A versus B trial.

Frequentist analysis for first A versus B trial

Comparing the proportion of errors made on the 1st A trial and B trial within each task, a within subjects t-test found performance was significantly better on the A trails than on B (Figure S7). On the first task ($t = 2.97$, $P = .004$), there was a mean probability of error on the A trial of 0.18 (SD = 0.39) and a mean probability of error of 0.39 on the B trial (SD = 0.49). On the second task ($t = 7.56$, $P < .001$), there was a mean probability of error on the A trial of 0.13 (SD = 0.34) and a mean probability of error of 0.61 on the B trial (SD = 0.49).

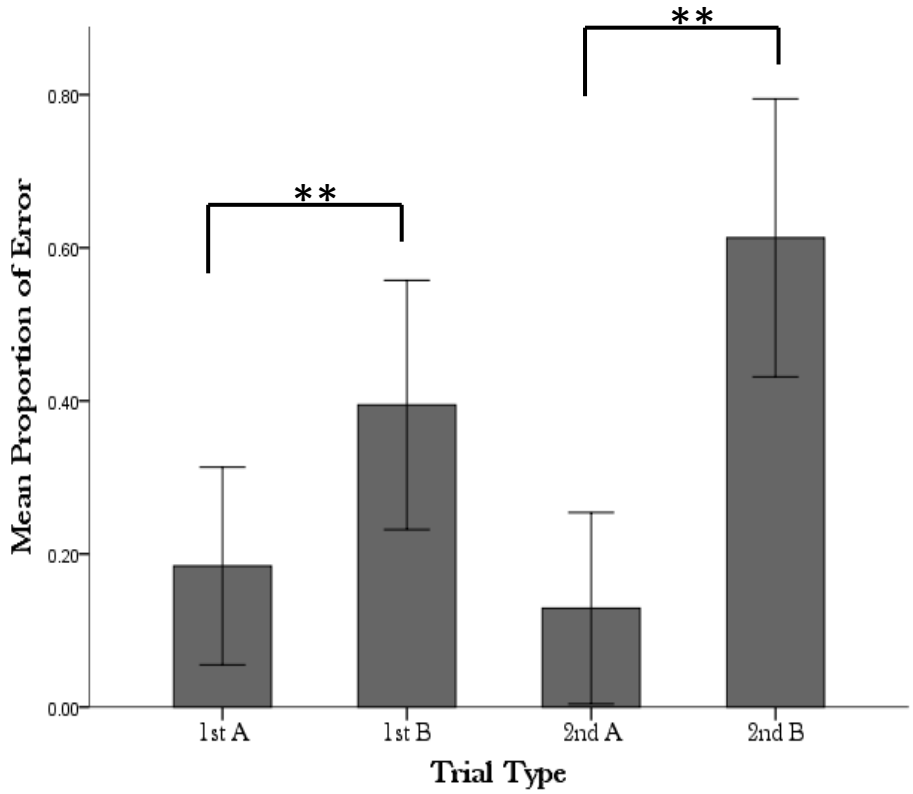


Fig. S7 Mean proportion of errors on 1st A and B trial on 1st and 2nd presentations. Error bars show the 95% confidence interval.

Errors on first A trial versus the B trial including an order effect

A model including a main effect of trial type (A or B) and an interaction between trial type and an order effect was found to best predict the data

$$Probability\ of\ error \sim Binomial\ (1, p)$$

$$Logit\ (p) \sim a + b * Trial\ type + bbord * Trial\ type * Order$$

Table S9 Coefficients of the model parameters for effect of first trial type (A or B) and order

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-1.55	0.43	-2.4	-0.72
Trial type	1.12	0.55	0.03	2.18
Order	-0.45	0.7	-1.89	0.87
Trial type*Order	1.36	0.85	-0.25	3.07

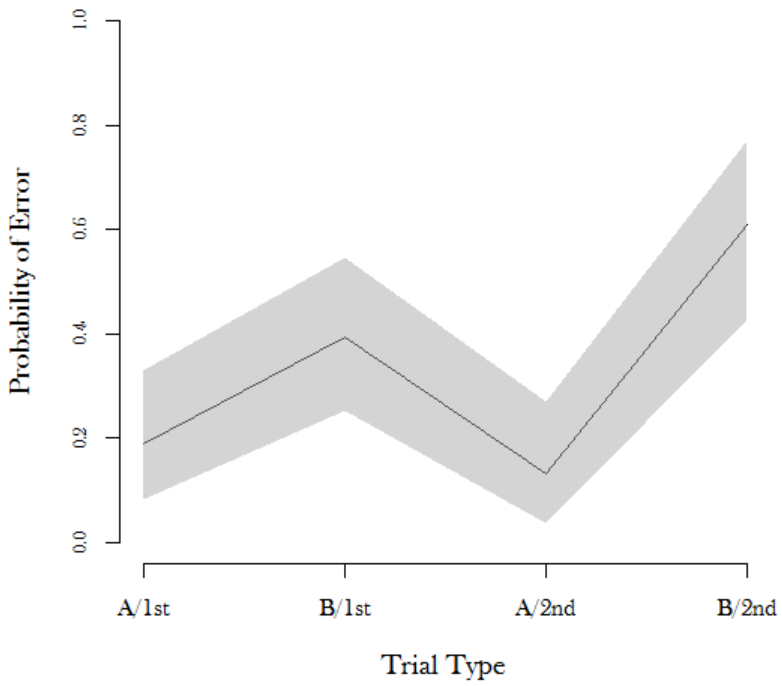


Fig S8 Regression predictions for trial type by order. The black line is the mean of the effect of trial type and order on the expected probability of a reaching error. The dark grey area is the 95% credible interval

Age and Error on B

Models were constructed with age to be predicted by reaching error

$$Age \sim Normal\ (mu, sigma)$$

$$mu \sim a + b * Error$$

While those who committed preservative errors tended to be older (median of 4.2 years, 95% credible interval of -1.65 to 10.12 years, this difference was not found to be credible (Tables S10 & S11; Figure S9)

Table S10 Coefficients of the model parameters for age and error on B

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	29.88	1.95	26.76	32.72
B (of error)	4.24	3.03	-0.61	9.09
Sigma	9.63	1.1	7.86	11.39

Table S11 Regression predictions for age and errors on B trials.

B Trial	Median	2.5%	97.5%
No Error	29.89	26.08	33.7
Error	34.13	29.4	38.82

Fig S9 Posterior distributions of age for error on B trial.

APPENDIX 3: BIWAYS AND PITFALL

BEHAVIORAL CONSERVATISM IS LINKED TO COMPLEXITY OF BEHAVIOR IN CHIMPANZEES: IMPLICATIONS FOR COGNITION AND CUMULATIVE CULTURE

CONTENTS PAGE

BIWAYS

Individual	Sex	Age	Group	Wild/captive	Rearing
Ma	F	49.39	Model	Wild	Unknown
My	F	50.39	IPSI	Wild	Unknown
Cea	F	24.23	IPSI	Captive	Mother
Ze	F	13.09	IPSI	Captive	Mother
Co	F	30.96	Model	Captive	Mother
Hh	F	24.64	IPIS	Captive	Mother
Cr	M	19.50	IPSI	Captive	Mother
Mi	F	25.09	Model	Captive	Mother
Sa	F	25.11	IPSI	Captive	Mother
Je	F	25.36	IPSI	Captive	Mother
Ti	M	26.08	IPSI	Captive	Mother
Kt	F	26.82	Model	Captive	Nursery
Na	F	24.92	SI	Captive	Nursery
Ae	F	40.43	SI	Wild	Unknown
Ci	F	24.48	SI	Captive	Nursery
Ai	F	20.25	Model	Captive	Nursery
Gs	M	23.46	SI	Captive	Nursery
Chu	F	34.62	SI	Captive	Mother
Hg	F	17.44	SI	Captive	Mother
Bn	M	33.85	IP	Captive	Mother
Tk	F	35.63	IP	Captive	Mother
Sy	F	43.97	IP	Wild	Unknown
Bte	F	37.83	IP	Captive	Mother
Pr	F	48.97	IP	Wild	Unknown
Pe	F	29.91	Naïve	Captive	Nursery
Di	F	30.47	Naïve	Captive	Mother
Sn	M	31.65	Naïve	Captive	Mother
Ki	M	34.30	Naïve	Captive	Mother
Ka	M	35.87	Naïve	Captive	Mother
Mpa	F	33.90	Naïve	Captive	Nursery
Ta	F	47.07	Naïve	Wild	Unknown
Kg	M	33.73	Naïve	Captive	Mother
Ti	M	21.98	Naïve	Captive	Mother

Table S1
Demographics of participants meeting criterion for inclusion. From left to right: Individual: Initials of participant (individuals are organised by their groups with participants listed under their respective models); Sex: F = female, M = male; Age: Age in years at time of testing; Group: Condition; Captive/wild: Captive = born in captivity, Wild = born in the wild; Rearing: Mother = raised by mother, Nursery = raised by human caretakers.

Group size ranged from 5-10 individuals. Chimpanzees were trained and tested in both their outside enclosures (ranging in size from corrals at 4,300 square feet to Primadomes™ measuring approximately 34 feet in diameter and 25 feet high) and indoor dens (ranging in size from 6 feet deep by 15 feet wide to approximately 8 feet and 8 inches deep by 9 feet wide). Individuals were given the opportunity to voluntarily participate and separate from their group for further training and testing purposes in their inside enclosures for a period of no longer than 30 minutes. Participants were not food or water deprived during training or testing.

STUDY 1.1: SUPPLEMENTARY METHODS

Model choice

The absence or presence of social information regarding the availability of an alternative solution was coded as 0 or 1 respectively. Models were generated through MCMC sampling (typically 6000 iterations; warmup of 1000 iterations). Given the small sample sizes, Gaussian regularizing priors were used with mean of 0 and standard deviation of 10. As only two outcomes were possible (slide or pull), the GLMM was based on a binomial distribution. Given multiple observations of each participant, partially pooled intercepts where used to account for individual variation in response. Assessing the best model was done with Widely Applicable Information Criterion (WAIC), along with posterior predictive checks.

GLMMs took the form:

$$1)\ Pull\ Total \sim Binomial\ (Total\ solutions, p)$$

$$Logit\ (p) < - x$$

With *x* including parameters based on:

i. Payoff: does increasing payoff affect the proportion of pull responses

ii. Social information: Does having social information of an alternative solution (pull) affect the proportion of pull behaviors

iii. An interaction between payoff and social information: Does the presence or absence of social information regarding an alternative solution (pull) interact with the presence of an increased payoff to affect the proportion of pull behaviors

Outcomes were thus modelled as comparisons between IPSI and SI groups to look for an effect of increased payoff on adopting that alternative solution (i above); as comparisons between IPSI and IP to look for an effect of social information of the availability of an alternative solution on adopting that solution (ii above); and as an interaction between social information of an alternative solution, and this solution having an increased payoff, on adopting this alternative solution (iii above); that is, is behavioral change dependent on both increased payoff and social information of an alternative solution.

STUDY 1.1 SUPPLEMENTARY RESULTS

Behaviors in testing phase

Individual	Group	IP	SI	Pull solutions	Total solutions
My	IPSI	Yes	Yes	281	296
Cea	IPSI	Yes	Yes	81	97
Ze	IPSI	Yes	Yes	68	68
Sa	IPSI	Yes	Yes	134	193
Je	IPSI	Yes	Yes	21	29
Ti	IPSI	Yes	Yes	25	59
Hh	IPSI	Yes	Yes	58	60
Cr	IPSI	Yes	Yes	83	207
Na	SI	No	Yes	0	298
Ci	SI	No	Yes	0	87
Ae	SI	No	Yes	0	209
Hg	SI	No	Yes	0	158
Chu	SI	No	Yes	1	155
Gs	SI	No	Yes	55	328
Bn	IP	Yes	No	0	115
Tk	IP	Yes	No	0	115
Sy	IP	Yes	No	0	115
Bte	IP	Yes	No	0	115
Pr	IP	Yes	No	0	115

Table S2

Behaviours in testing phase. From left to right: Individual: Initials of participant; Group: IPSI = increased payoff with social information, SI = same payoff with social information, IP = increased payoff with no social information; IP: Did the pull solution result in an increased payoff? SI: Was social information about the alternative pull solution available? Pull: total number of pull solutions. Total: all solutions used, including pull, slide and both.

The relationship between predictors and outcome can be modelled as

$$1)\ Pull\ Total \sim Binomial\ (Total\ solutions, p)$$

$$Logit(p) < -a + a[Individual] + bip * IP + bsi * SI + bipsi * IP * SI,$$

Where *a* is the value of the average intercept, *a [individual]* is the intercept deviance for each participant (allowing partially pooled variance), *bip* is the value of the coefficient of the effect of increased payoff, *bsi* is the value of the coefficient of the effect of the presence of social information, and *bipsi* is the value of the coefficient of the interaction between the presence of a solution with an increased payoff (*IP*) and the presence of social information (*SI*) regarding the availability of an alternative solution (Coefficients are summarized in Table S3, along with their 95% credible intervals). Models which did not include the main effects, that is, just the interaction effect, resulted in almost equal effectiveness, indicating that outcome is largely affected by only this interaction (Table S4). The full model was chosen as it gets most of the Akaike weight. This model closely retrodicted the observed data. This model also simulated data which matched observed data (Figure S1).

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	-10.40	5.63	-21.55	0.38
bip	-3.15	5.59	-14.06	7.83
bsi	3.98	5.62	-6.68	15.18
bipsi	11.3	5.64	0.06	22.39

Table S3

Coefficients of the model parameters for effect of payoff and social information. Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
Full model	1185.5	9.4	0	0.61	48.42	NA
Interaction only	1186.4	9.8	0.9	0.39	48.7	0.78

Table S4
Model comparison. WAIC is the Widely Applicable Information Criterion; pWAIC indicates the number of effective parameters; dWAIC is the difference in WAIC values; Weight is the Akaike weight and indicates the effectiveness of the model to describe the data; SE is the standard error of the WAIC estimate; dSE is the standard error of the difference in WAIC of models (McElreath, 2016)

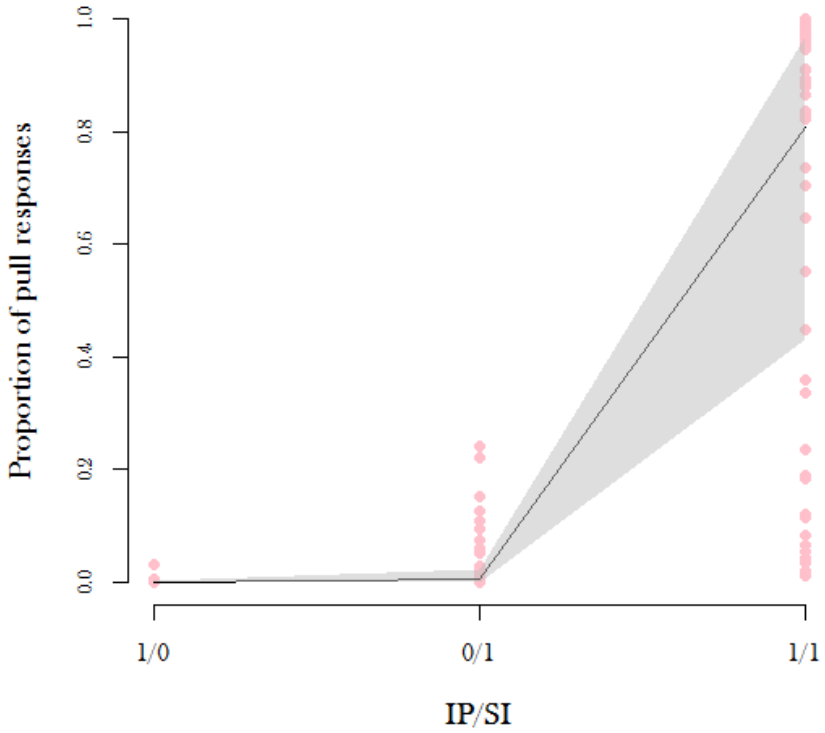


Fig S1. Simulated data. Proportion of pull responses for presence (1) or absence (0) of increased payoff (IP) and social information (SI) respectively. The line represents the mean effect of condition, with the shaded area showing the 95% credible interval where the mean could lie. The pink circles are the proportion of pulls for 50 simulated participants in each condition.

STUDY 1.2. SUPPLEMENTARY RESULTS

A log-liner regression model of the form

$$\log(Solutions\ taken\ until\ convergence\ on\ Pull\ solution) \sim dnorm(\ mu, sigma)$$

$$mu < -a + b * Experience$$

produced the coefficients summarized in Table S5, where a is the expected solutions till convergence for naïve individuals, and b is the effect of having experience with a prior, sub-optimal behavior on solutions taken. Due to small samples sizes, the prior start values for the parameters were set at values closely approximating the median and standard deviation of observed solutions before converging on the pull solution taken by the naive group (0 and 1 respectively). The effect of experience is shown in Figure S2. Model comparison between models which include or exclude having a prior solution as a factor influencing convergence of the optimum solution is summarized in Table S6.

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept (*a*)	0.76	0.44	0.06	1.45
Effect of experience (*b*)	1.71	0.67	0.64	2.78
Sigma	1.45	0.25	1.05	1.85

Table S5
Coefficients of the model parameters for effect of experience. Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

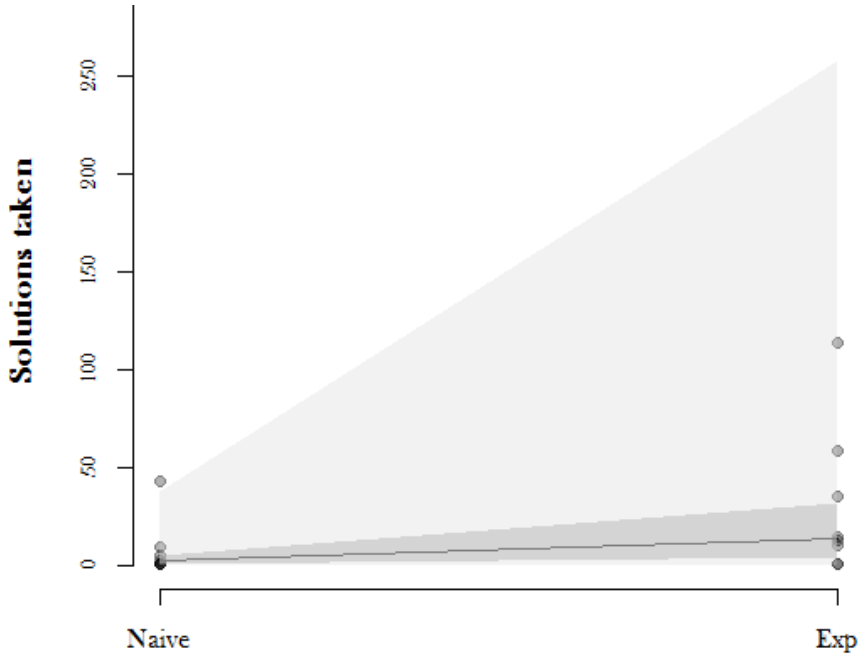


Fig S2. Model predictions for solutions taken before converging on the optimum behaviour for naïve and experienced individuals. The line is the mean of the modelled effect, with the dark shaded area showing 95% credible interval of where the mean may lie. The light grey shading is where the model predicts 95% of solutions taken will lie in the population

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
With prior exp	69.4	4.2	0	0.58	7.02	NA
Without prior exp	70.1	2.2	0.7	0.42	4.64	6.2

Table S6
Model comparison for inclusion and exclusion of the effect of having a prior, sub-optimal solution on convergence on the optimum pull behavior.

Bayesian estimation. To examine if having a prior solution had an effect of behavioral optimization, the number of attempts taken to converge on the optimum solution (Pull) was compared between IPSI individuals and SN individuals using Bayesian Estimation (online software: http://www.sumsar.net/best_online/ for a Bayesian version of the t-test developed by John Krueschke, 20000 burn in and 80000 iterations (Kruschke, 2013)).

It was found that the 95% credible interval for differences between the mean number of solutions taken by experience and naïve individuals to converge on the solution crossed the boundary of zero (mean of 16.9 and range -7.54 - 46.3), indicating that having a prior solution may not have had an effect on behavioral optimization.

Frequentist analysis. A Mann Whitney U test revealed no effect of having a prior solution on convergence on the optimum solution (Figure S3; $U = 17$, Wilcoxon $W = 62$, $Z = -1.894$; P=.064 (two tailed). There was however a trend towards significance. The effect size is 0.46 (as given by $Z/\sqrt{N}$, where N is the total observations considered in the analysis)

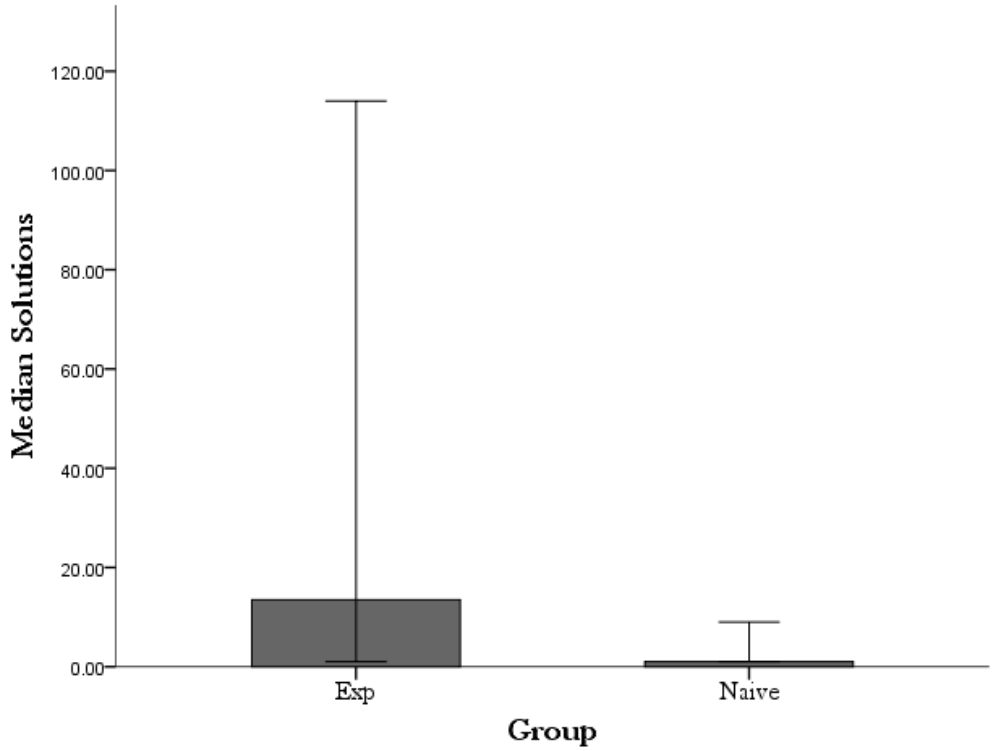


Fig S3. Median solution on which IPSI (Exp) and SN (Naïve) groups converged on the optimum solution. Error bars show the 95% confidence interval.

PITFALL

PARTICIPANT DEMOGRAPHICS

Individual	Sex	Age	Group	Wild/captive	Rearing
Ma	F	49.89	Model	Wild	Unknown
My	F	50.89	IPSI	Wild	Unknown
Cea	F	24.73	IPSI	Captive	Mother
Al	M	35.78	IPSI	Captive	Nursery
Co	F	31.22	Model	Captive	Mother
Hh	F	24.91	IPIS	Captive	Mother
Cr	M	19.76	IPSI	Captive	Mother
Kt	F	27.19	Model	Captive	Nursery
Na	F	25.29	IPSI	Captive	Nursery
Ae	F	40.81	IPSI	Wild	Unknown
Ci	F	24.86	IPSI	Captive	Nursery
Ai	F	20.74	Model	Captive	Nursery
Gs	M	23.94	IPSI	Captive	Nursery
Sa	F	25.28	IPSI	Captive	Mother
Jy	M	43.95	IP	Wild	Unknown
Oi	F	31.08	IP	Captive	Mother
Ji	M	25.28	IP	Captive	Nursery
Tk	F	35.60822	IP	Captive	Mother
Pr	F	48.94795	IP	Wild	Unknown
Ta	F	47.02466	IP	Wild	Unknown
Ki	M	34.22192	Naïve	Captive	Mother
Mpa	F	33.8274	Naïve	Captive	Nursery
Di	F	30.38904	Naïve	Captive	Mother
Pe	F	29.8274	Naïve	Captive	Nursery
Sn	M	31.57534	Naïve	Captive	Mother
Kg	M	33.71507	Naïve	Captive	Mother
Ti	M	21.95616	Naïve	Captive	Mother
Eo	M	20.27123	Naïve	Captive	Nursery

Table S7
Demographics of participants meeting criterion for inclusion. From left to right: Individual: Initials of participant (individuals are organised by their groups with participants listed under their respective models); Sex: F = female, M = male; Age: Age in years at time of testing; Group: Condition; Captive/wild: Captive = born in captivity, Wild = born in the wild; Rearing: Mother = raised by mother, Nursery = raised by human caretakers.

STUDY 2.1. SUPPLEMENTARY RESULTS

Coefficients of a log-linear regression model, with the inclusion of group (Social or asocial) are summarized in Table S8. Due to small samples sizes, the prior start values for parameters were set at values closely approximating the median and standard deviation (0 and 1 respectively) of the log of observed solutions before converging on the Door B solution taken by the IPSI (social) group. One IP (asocial control) individual (*Oi*) never discovered Door 1. It was assumed, given she was the only IP individual to fail to do so, that this may have been due to not being given enough time with the apparatus, and that it was likely she would have eventually done so. Due to this, *Oi* was conservatively assigned an estimate of when she may have discovered Door 1 as being on her next solution attempt, had this opportunity been provided. Model predictions for groups are shown in Figure S4. Model comparison between models which include or exclude social information as a factor influencing convergence on the optimum solution is summarized in Table S9.

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	1.17	0.32	0.65	1.69
Effect of social info	1.59	0.51	0.77	2.4
Sigma	1.14	0.21	0.81	1.47

Table S8
Coefficients of the model parameters for effect of social information. Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
With social info	57.5	3.5	0	0.96	5.07	NA
Without social info	63.9	2.5	6.6	0.04	5.61	5.25

Table S9.
Model comparison for inclusion and exclusion of social information.

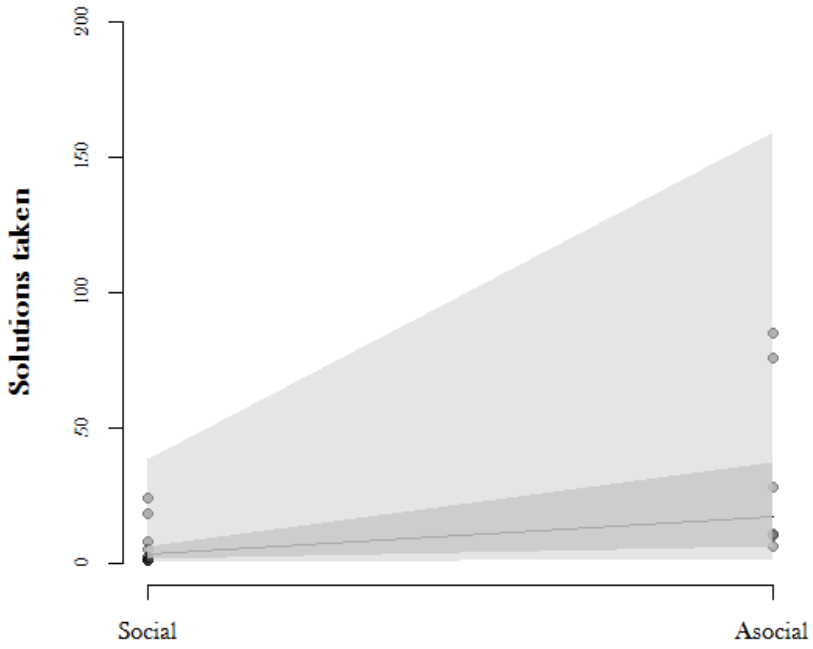


Fig S4. Model predictions of solutions taken before converging on Door 1 solution for social/IPSI and asocial/IP individuals.

Bayesian estimation. To examine if having social information had an effect of behavioral optimization, the number of attempts taken to converge on the optimum solution (Door 1 solution) was compared between IPSI individuals and SN individuals. It was found that the 95% credible interval for differences between the mean number of trials to converge on the solution did cross the boundary of zero (mean of 29 additional solutions for asocial; range - 15.1 and 73.6), indicating that social information may not have had a credible effect on solution optimization.

Frequentist analysis. A Mann Whitney U test found a significant effect of social information on solutions taken before converging on the optimum Door 1 solution ($U = 7$, $W = 62$, $Z = -2.52$, P =0.01, effect size = 0.63)

BEHAVIORAL VARIANTS

		Block			Block		Door 1		Food order	
Individual	Trained solution	Sequence	Pre-empt	Door 1 solution	Sequence	Pre-empt	Sequence	Pre-empt	Small first	Large first
My	0	0	0	102	81	21	85	17	86	15
Cea	0	0	0	35	29	6	34	1	31	4
Al	23	19	4	94	90	4	93	1	20	71
Na	17	2	15	78	47	31	73	5	61	9
Ci	7	6	1	23	20	3	21	2	22	1
Ae	1	0	1	53	48	5	53	0	27	26
Sa	6	6	0	32	29	3	29	3	28	3
Gs	1	1	0	54	42	12	49	5	44	8
Hh	0	0	0	63	43	20	62	1	28	35
Cr	1	0	1	78	74	4	76	2	67	4

Table S10

Solution variants during Study 2.1 testing. Table cells are colored pink for data relating to the Trained solution. From left to right: Individual: Initials of participants; Trained solution: Number of times the participant used the Trained solution; Block – Sequence: number of times the block defense was pushed out only once the foodbox arrived at the block's location when using the Trained Solution; Block – Pre-empt: the number of times the block defense was pre-emptively removed before the foodbox arrived at the block's location; Door 1 solution: Number of times the participant used the Door 1 solution; Block – Sequence: number of times the block defense was pushed out only once the foodbox arrived at the block's location when using the Door 1 Solution; Block – Pre-empt: the number of times the block defense was removed pre-emptively; Door 1 – Sequence: the number of times Door 1 was opened only when the foodbox arrived at Door 1's location; Door 1 – Pre-empt: the number of times Door 1 was pre-emptively opened before the foodbox arrived at Door 1's location. Food order – Small first: the number of times the small reward was removed from the foodbox before the large reward; Food order – Large first: the number of times the large reward was removed from the foodbox before the small reward.

PITFALL: STUDY 2.2

Converging on the optimum Door B solution for IPSI and solution naïve individuals. A log-linear regression model, with the inclusion of group (naïve or experienced) produced the coefficients summarized in Table S11. Due to small samples sizes, the prior start values for parameters were set at values closely approximating the median and standard deviation of the log of observed solutions before converging on the Door B solution taken by the naive group (0 and 1 respectively). The posterior densities for groups are shown in Figure S5, revealing an unlikely overlap in predicted values for the naïve and experienced groups. Model comparison between models which include or exclude having a prior solution as a factor influencing convergence on the optimum solution is summarized in Table S12.

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	0.27	0.28	-0.17	0.72
Effect of experience	2.47	0.37	1.87	3.07
Sigma	0.83	0.14	0.6	1.06

Table S11
Coefficients of the model parameters for effect of experience. Mean is the mean predicted value of the coefficient. StdDev is the standard deviation. Lower 0.95 and upper 0.95 are the 95% credible interval boundaries for the coefficient values.

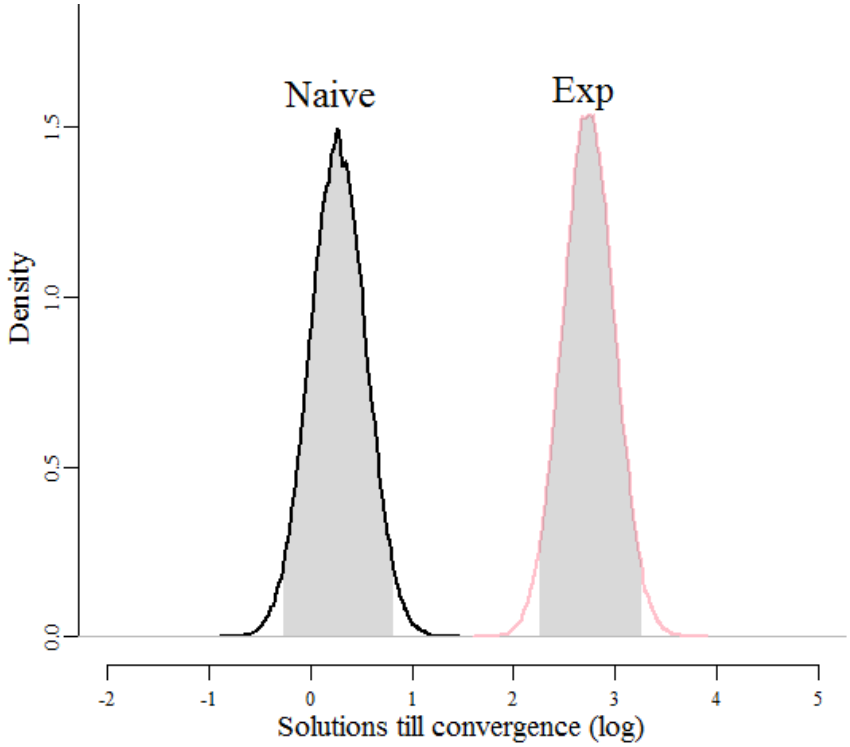


Fig S5. Posterior distributions of solutions taken before converging on the optimum solution for naïve (black) and experienced (pink) individuals. Light grey shading shows the 95% highest posterior density interval for each group.

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
With prior exp	52.8	4.2	0	1	8.02	NA
Without prior exp	73.34	1.9	20.5	0	4.84	7.39

Table S12.
Model comparison for inclusion and exclusion of prior solution.

Bayesian estimation. To examine if having a prior solution had an effect of behavioral optimization, the number of attempts taken to converge on the optimum solution (Door 2 solution) was compared between IPSI individuals and solution naïve individuals. It was found that the 95% credible interval for differences between the mean number of solutions to converge on the optimum did not cross the boundary of zero (mean of 23.2 and range - 6.51- -39.2), indicating that prior solution had an effect on solution optimization.

Frequentist analysis. A Mann Whitney U test found a significant effect of prior knowledge of a complex, sub-optimal solution on converging on the optimum solution (Figure S6; U=0, W= 36, Z= - 3, P<0.0001), with an effect size of 0.71.

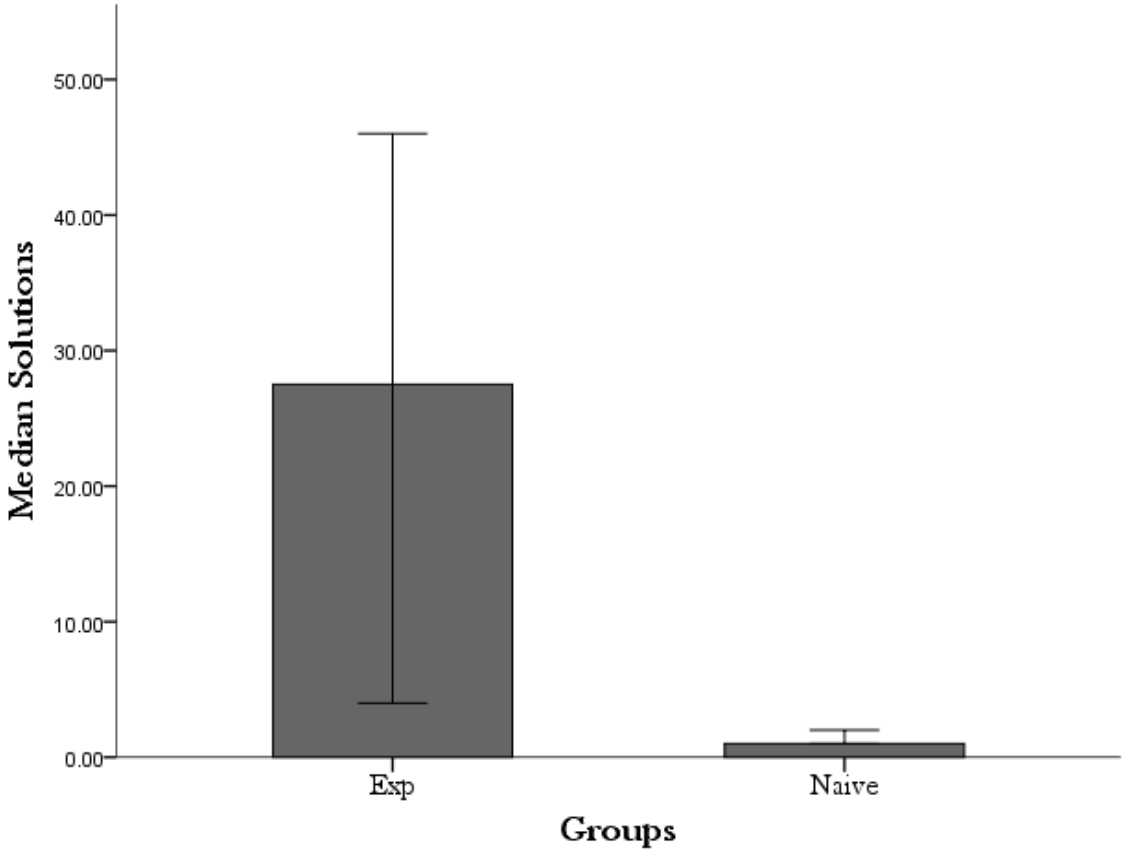


Fig S6. Median solution on which IPSI (Exp) and SN (Naïve) groups converged on the optimum solution. Error bars show the 95% confidence interval.

Converging on the optimum Door 2 and Door 1 solution for IPSI individuals. A log-linear regression model, with the inclusion of door location (Door 1 or Door 2) produced the coefficients summarized in Table S13. Due to small samples sizes, the prior start values for parameters were set at values closely approximating the median and standard deviation of the log of observed solutions before converging on the Door B solution (0 and 1 respectively). The posterior densities for solutions are shown in Figure S7, revealing an unlikely overlap in predicted solutions taken before convergence on the Door 1 and Door 2 solutions. Model comparison between models which include or exclude door (1 or 2) as a factor influencing convergence on the optimum solution is summarized in Table S14.

Parameters	Mean	StdDev	Lower 0.95	Upper 0.95
Average intercept	1.16	0.32	0.65	1.68
Effect of door	1.55	0.45	0.84	2.26
Sigma	1.13	0.18	0.84	1.42

Table S13
Coefficients of the model parameters for effect of door location.

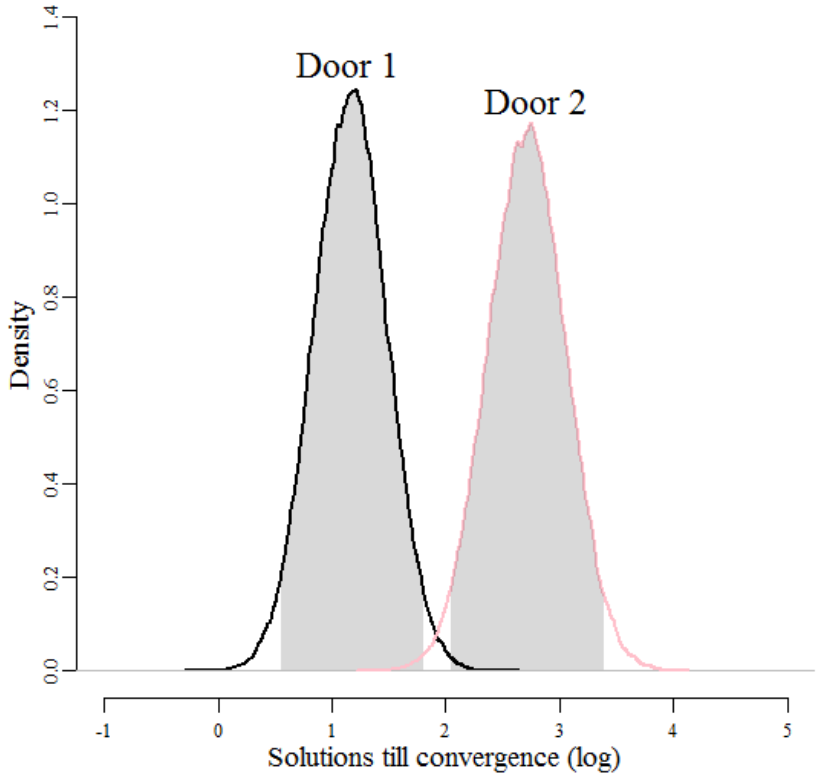


Fig S7. Posterior distributions of solutions taken before converging on the optimum solution of using Door 1 (black) and Door 2 (pink) for IPSI individuals.

Model	WAIC	pWAIC	dWAIC	Weight	SE	dSE
With door	68.6	3.2	0	0.97	5.02	NA
Without door	75.9	1.8	7.3	0.03	4.69	5.93

Table S14
Model comparison for inclusion and exclusion of door location.

Bayesian estimation. To examine if having to inhibit a prior solution (Door 2 solution) versus having to build on it (Door 1 solution) had an effect on behavioral optimization, the number of attempts taken to converge on the optimum solution (Door 1 and 2 solutions) was compared within IPSI individuals. It was found that the 95% credible interval for differences between the

mean number of solutions taken to converge on the Door 1 and Door 2 solutions did not cross the boundary of zero (mean of -22; range –44.3 - -1.11), indicating that the Door 1 solution was adopted after fewer solution attempts than the Door 2 solution by IPSI individuals.

Frequentist analysis. A Wilcoxon signed rank test found a significant effect of door location (Door 1 (no inhibition required) and Door 2 (inhibition required)) on convergence rate (Z = -2.8, P<0.001 (one tailed), indicating it took more solution attempts to begin using Door 2 than it did Door 1.

REFERENCES

Kruschke, J. (2013). Bayesian estimation supersedes the t-test. *Journal of Experimental Psychology: General*, *142*(2), 573–603. https://doi.org/10.1037/a0029146

McElreath, R. (2015). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*. Chapman & Hall. CRC Press.

FOUNDATIONS OF CUMULATIVE CULTURE IN APES: IMPROVED FORAGING EFFICIENCY THROUGH RELINQUISHING AND COMBINING WITNESSED BEHAVIOURS IN CHIMPANZEES (*PAN TROGLODYTES*)

	Group	Total	Efficient	Median	Range
Training	Social	254	0	21	20-32
	Non-seeded	202	0	23	20-37
Test period 1	Social	496	189	22	2-179
	Non-seeded	299	0	39.5	4-81
Test period 2	Social	440	362	15	2-194
	Non-seeded	235	144	15	2-145
Test period 3	Social	418	324	13	0-117
	Non-seeded	154	84	9	0-84

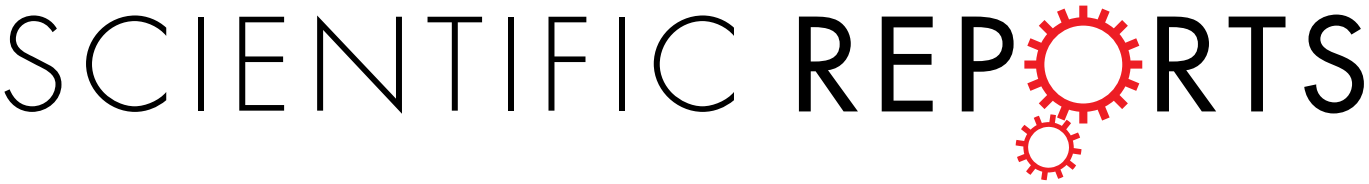
Supplementary Table S1. Extractions by participants across test periods. 'Total' is the sum of extractions made by all participants in the 'social information' and 'non-seeded' groups; 'Efficient' is the sum of efficient extractions; 'Median' is the median number of extractions; 'Range' is the range of extractions.

	Model	Total	Median	Range	Efficiency
Experiment 1	My	90	24	13-29	33.3
	Co	65	18	11-18	4.1
	Mi	134	46	34-56	11.9
Experiment 2	My	97	24.5	11-37	70.1
	Co	8	1.5	1-4	90.2
	Mi	156	52	32-72	92.2

Supplementary Table S2. Summary of models' behaviours. Extraction data is presented based on group observations of their respective models. Models are identified by their initials. 'Total' is the sum of participants' observations of extractions made by their model. 'Median' is the median number of observed extractions made by the model. 'Range' is the range of the sum of participant observations of extractions made by the model. For Experiment 1, the total, median and range figures include extractions observed during the social demonstration phase in addition to those observed during Experiment 1 testing period. 'Efficiency' (in seconds) is the difference of the model's mean latency to extraction relative to the median of participants' mean investment in using the inefficient method (i.e. includes times spent performing the inefficient method whether the participant was successful or not in extracting the token), and reflects how much faster the efficient method was compared to the inefficient.

Individual	Group	Exp1: Obs	Exp1: Extract	Exp2: Obs	Exp2: Extract	HD: Obs	HD: Extract	Switch: Obs	Switch: Extract
Sa	Social info	**21**	**0**	N/A	N/A	N/A	N/A	21	1
Se	Social info	**15**	**6**	N/A	N/A	N/A	N/A	15	7
Ze	Social info	29	4	**15**	**4**	N/A	N/A	44	9
Cr	Social info	11	10	2	3	**17**	**16**	30	30
Ma	Social info	27	33	**15**	**2**	N/A	N/A	42	36
An	Social info	19	16	5	2	**17**	**16**	41	35
Je	Social info	57	18	102	14	**10**	**9**	169	42
Kt	Non-seed	0	81	**0**	**1**	N/A	N/A	0	83
Cea	Social info	13	67	**9**	**17**	N/A	N/A	22	85
Hh	Social info	18	119	1	19	**12**	**11**	31	150
Si	Social info	45	2	49	7	12	12	106	No switch
Ta	Social info	21	22	18	3	N/A	N/A	39	No switch
Na	Non-seed	0	49	3	20	N/A	N/A	3	No switch
Ae	Non-seed	0	4	2	7	N/A	N/A	2	No switch
Ai	Non-seed	0	55	0	20	N/A	N/A	0	No switch
Gs	Non-seed	0	58	0	2	N/A	N/A	0	No switch
Chu	Non-seed	0	30	0	18	N/A	N/A	0	No switch
Sha	Non-seed	0	6	0	12	N/A	N/A	0	No switch
Ka	Non-seed	0	16	0	11	N/A	N/A	0	No switch

Supplementary Table S3: Observation and extraction data for each individual. From left to right: 'Individual' is the participant represented by their initials and organised in ascending order of total number of inefficient extractions experienced before switching to the efficient solution (final column); Group: 'Social info' = 'social information' group; 'Non-seed' = 'non-seeded' group. 'Exp1: Obs' and 'Exp2: Obs' are the number of observations of the efficient method for each individual before they switched to the efficient method in each experimental condition respectively. 'Exp1: Obs' includes observations from the 'social demonstration phase'. 'Exp1: Extract' and 'Exp2: Extract' are the number of extractions in which a participant successfully extracted or attempted to extract the token before switching to use of the efficient method. 'N/A' denotes the data during this experimental phase are not applicable to the participant's switching behaviour. 'HD: Obs' and 'HD: Extract' are the number of observations and extractions experienced in the 'Human Demonstration' phase of Experiment 2 respectively. 'Switch: Obs' is the total number of observations across experimental phases before switching to the efficient method. These data include observations of the model, of other participants and, where applicable, human demonstrations of the efficient method. If the individual did not switch, this number is the total number of observations across experimental phases 'Switch: Extract' refers to the extraction attempt the individual switched on and includes extractions across all experimental phases. The experimental phase in which the participant switched is reflected with the emboldening and underlining of the number of efficient extractions observed and the number of extractions experienced pre-switch.



OPEN

Received: 01 April 2016
Accepted: 05 October 2016
Published: 24 October 2016

Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*)

Sarah J. Davis[1,2], Gillian L. Vale[1,2], Steven J. Schapiro[2], Susan P. Lambeth[2] & Andrew Whiten[1]

A vital prerequisite for cumulative culture, a phenomenon often asserted to be unique to humans, is the ability to modify behaviour and flexibly switch to more productive or efficient alternatives. Here, we first established an inefficient solution to a foraging task in five captive chimpanzee groups ($N = 19$). Three groups subsequently witnessed a conspecific using an alternative, more efficient, solution. When participants could successfully forage with their established behaviours, most individuals did not switch to this more efficient technique; however, when their foraging method became substantially less efficient, nine chimpanzees with socially-acquired information (four of whom witnessed additional human demonstrations) relinquished their old behaviour in favour of the more efficient one. Only a single chimpanzee in control groups, who had not witnessed a knowledgeable model, discovered this. Individuals who switched were later able to combine components of their two learned techniques to produce a more efficient solution than their extensively used, original foraging method. These results suggest that, although chimpanzees show a considerable degree of conservatism, they also have an ability to combine independent behaviours to produce efficient compound action sequences; one of the foundational abilities (or candidate mechanisms) for human cumulative culture.

Culture has been defined as "group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information" (p.151[1]). The ability to build upon or ratchet up on such cultural behaviours, creating cumulative cultural change[2], can lead to substantial gains in productivity or efficiency, well exemplified in its elaboration in humans[3]. Whilst the ability to socially learn behaviours (defined as "learning that is influenced by observation of, or interaction with another animal (typically a conspecific) or its products" (p.207[4]) may be common across many animal taxa[5–9], cumulative culture is limited or, according to some authors, absent in non-human animals[2,3,10]. This is most striking when we compare our human cultures with those of arguably the second most cultural species, our closest living relative, the chimpanzee (*Pan troglodytes*)[11].

Chimpanzees exhibit the greatest number of traditions outside of the human species, across foraging, tool use and social behaviours, with each chimpanzee group distinguished by their own particular cultural profile[11]. Yet, there is little evidence for cultural accumulation on these traditions (see ref. 12). Various factors may contribute to the stasis of chimpanzee culture, such as relevant socio-cognitive adaptations[13], low fidelity social learning mechanisms[14], or failure to employ appropriate learning heuristics[15,16]. However, cumulative culture ultimately requires the ability to change established behaviours in order to adopt more efficient or productive ones; that is, in order to upgrade solutions, an individual must possess the behavioural flexibility to relinquish, modify and build on prior solutions. Behavioural inflexibility may therefore, in and of itself, limit the evolution of culture. With behavioural flexibility defined as "the continued interest in and acquisition of new solutions to a task, through

[1]Centre for Social learning and Cognitive Evolution, School of Psychology & Neuroscience, University of St Andrews, St Andrews, KY16 9JP, Scotland. [2]National Center for Chimpanzee Care, Department of Veterinary Sciences, Michale E. Keeling Center for Comparative Medicine and Research, the University of Texas MD Anderson Cancer Center, Bastrop, TX 78602, USA. Correspondence and requests for materials should be addressed to A.W. (email: aw2@st-andrews.ac.uk)

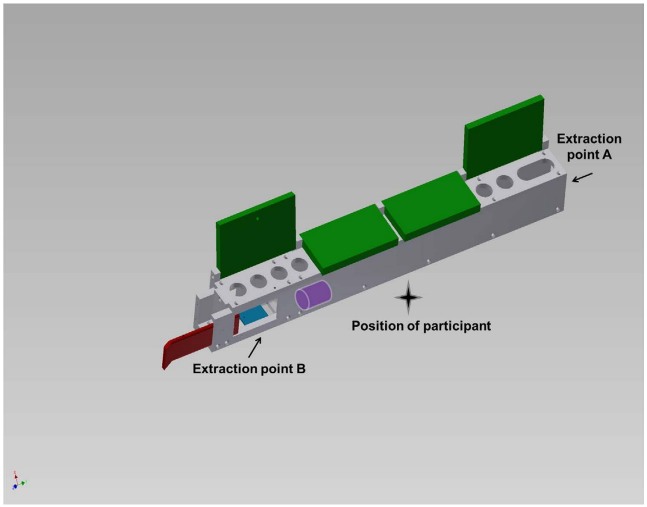


Figure 1. Serialbox. Along the length of the transparent Serialbox were four compartments. Each compartment had a hinged lid on top which could be lifted open (coloured here in green for image clarity; in reality all parts were transparent). Under each lid were four finger holes that permitted an object (depicted as a purple cylinder) initially provisioned in the left-most compartment to be pushed the length of the apparatus. This object could then be extracted through an opening at the other end ('Extraction point A'). This was the inefficient method in Experiments 1 and 3. A small door spanning two thirds of the first compartment (coloured here in red for clarity) was fitted on the chimpanzee side of the apparatus and could be pulled open using a handle protruding from the outside of the box to give alternative and quicker access to the left-most compartment ('Extraction point B'), where the token was initially positioned. This, in combination with lifting the lid of the left-most compartment and using the underlying holes to manoeuvre the token to extraction point B, was the efficient method in Experiments 1 and 3. The blue square shown in the left-most compartment depicts the indent in the floor in which the token was placed throughout Experiment 2.

either innovation or social learning, after already having mastered a previous solution" (p.447[17]), a lack of such flexibility has been found in several experiments with chimpanzees. Marshall-Pescini and Whiten[16] found that young chimpanzees failed to cumulatively modify their foraging efforts by building on their exisiting behaviours despite witnessing a more productive solution. Yet, the more complex behaviour could be acquired if participants had no prior knowledge of the less lucrative foraging technique. This led the authors to suggest that chimpanzees are behaviourally conservative, since reported in several further studies[13,18–21] (see also ref. 22); in simple terms, chimpanzees tend to become 'stuck' on known behaviours despite availability of superior alternatives.

These results appear inconsistent with other findings such as that of Horner and Whiten[23], where chimpanzees 'streamlined' their behaviours after witnessing inefficient options used by others. However, this involved omitting elements[24,25], as opposed to the additive, ratchet effect required for cumulative culure[2]. Similarly, following social demonstrations in a juice acquiring task, Yamamoto, Humle and Tanaka[26] found that chimpanzees switched from using a straw as a dipping tool to exploiting a more efficient sucking function, but this also did not involve additive ratcheting. Such findings are in line with records of behavioural modification in the wild[27–31] (see also ref. 32), as well as more recent experiments demonstrating payoff-related variation in simple behaviour, such as depositing 'tokens' in novel locations to increase food reward value[33,34].

From studies examining behavioural change in humans, we might expect at least two factors to have differential effects on behavioural flexibility: the extent to which behaviour has been practiced, and the complexity of the behaviour involved[35–37]. As cultural traditions are often well-established and long-held behaviours, and are also sufficiently complex to necessitate social learning to acquire them, it may be important to consider how well-ingrained the behaviour to be modified is when extrapolating results to chimpanzees' potential for cumulative culture. Evidence now exists that chimpanzees can recognise and adopt superior variants of behaviours which are simple and conceptually similar to existing routines[33,34]. Chimpanzees can also relinquish old solutions and build on very simple behaviours to form action sequences when these sequences are within most chimpanzees' repertoires[38], as well as relinquish behaviours that have been performed but not yet adopted as a reliable foraging strategy[23,26]. However, the extent to which chimpanzees can modify, relinquish or build-upon well-established, cognitively more complex behaviours, those that perhaps mirror cultural behaviours more closely, remains to be established[13,16].

In the present studies, we investigated chimpanzees' ability to build upon socially acquired, complex behaviour in the context of improving efficiency. Of particular interest is whether a chimpanzee can benefit by witnessing a more efficient behaviour used by a conspecific compared to one they currently reliably employ to achieve the same goal, and flexibly switch to using this more efficient behaviour.

A transparent puzzle box (Fig. 1) was used (hereafter 'Serialbox') from which a valued token could be extracted (later exchanged for a food reward) via either of two alternative operations differing in efficiency, with the inefficient method (Supplementary Video 1) more labour intensive and taking longer to complete. The efficient

method (Supplementary Video 2) involved partial use of behaviours common to the inefficient method, along with the addition of a novel behaviour. The efficient method therefore involved not only streamlining the inefficient method by a *subtractive* process (noted in some studies of cumulative culture)[24,25], but also the *addition* of a novel behavioural element to an established sequence, that is, a ratcheting up on behaviour[2]. Participants across five groups were initially trained to extract a valued token from the transparent Serialbox via a multi-stepped, repetitive, inefficient process (Fig. 1). To strengthen ecological validity when assessing chimpanzees' cumulative cultural capabilities, this extraction process was completed a minimum of 20 times over several sessions until it became a reliable and ingrained response. Three groups ('social information' groups) subsequently witnessed a conspecific model using the more efficient solution described in Fig. 1 and more fully in Methods below. Following repeated social demonstrations, the behaviour of participants was examined over ten hours of open diffusion, monitoring any spread of the more efficient technique, to better simulate the diffusion of behaviours in a culturally relevant context[39].

We hypothesised that if chimpanzees could recognise a solution more efficient than the one they were currently employing and were able to switch to this, they should do so once they witnessed the actions of the model, regarded as a simulated 'innovator'[40]. To assess how readily chimpanzees could themselves innovate and switch to the efficient method without the need for social information, we trained two control groups to use the inefficient method but did not expose them to the efficient method through a trained conspecific ('non-seeded' groups). To investigate how naïve chimpanzees might solve this extractive problem when they did not have an established solution to the puzzle, the Serialbox was introduced to one additional control group who were not initially trained to extract via the inefficient method ('naïve' group). For this group, the problem could be solved by using either the efficient or inefficient strategy.

Experiment 1: Results

Due to limited sample sizes, data were analysed using non-parametric methods with exact P values reported. Effect sizes were calculated using the Z score of the test statistic such that $r = Z/\sqrt{N}$, where N was the total number of observations included in the analysis. An analysis of interrater reliability using Cohen's kappa found excellent agreement ($\kappa = 1$) between two coders' judgement of whether the participant was extracting via the inefficient or the efficient method.

Participant inclusion and extractions across training and test phase. Eleven individuals in the 'social information' groups and eight in 'non-seeded' control groups met criterion for inclusion in the study (a minimum of 20 inefficient extractions; see Table 1 for participant demographics; Supplementary Table S1 for behaviours in the training and test periods; Supplementary Table S2 for relative efficiency of the two extraction techniques). There was no difference in the acquisition of the inefficient method between the 'social information' and 'non-seeded' individuals in terms of number of extractions made during the training period (Mann Whitney $U = 36$, $P = 0.529$; Supplementary Table S1).

Within the 'social information' groups, to analyse any growing behavioural proficiency, the mean time taken across the first ten extractions using the inefficient method was compared to the mean time taken across the last ten inefficient extractions, using a one-tailed Wilcoxon signed rank test. If an individual did not extract 20 times during the testing period, the mean times taken for inefficient extractions either side of the median extraction were calculated and compared. Individuals became significantly more proficient at the inefficient method over this test period ($Z = -2.803$, $n = 10$, $P = 0.001$, $r = -0.63$), with a median reduction in extraction latency from 47.5 to 26.2 seconds.

Switching behaviours. Across this testing period ('E1'), nine of the 11 individuals in the 'social information' groups and all individuals in the 'non-seeded' groups continued to exclusively use the inefficient method established during the training period ('E0') to extract the token.

To test for switching behaviour at the individual level, following van Leeuwen *et al.*[34], the number of inefficient and efficient extractions performed during E0 and E1 were compared using a one-tailed Fisher's exact test. Two individuals (from separate groups) demonstrated a significant change of behaviour within this period, switching to using the efficient solution (Individual *Se*: $E0_{0,21}$, $E1_{10,16}$, $P = 0.001$; Individual *Sa*: $E0_{0,22}$, $E1_{179,0}$, $P < 0.0001$: subscripts represent frequencies of efficient and inefficient methods respectively).

'Naïve' group. One individual, *Jy,* discovered and used the efficient method within two hours of interaction with the Serialbox. Individual *Ua* observed *Jy*'s efficient method five times; following three initial failed attempts to open the door, she successfully used the efficient method to extract the token in a subsequent test session. Before *Ua* witnessed use of the efficient method, she had unsuccessfully interacted with the apparatus, exploring only the holes and lids. Two other individuals witnessed the use of the efficient method just one and five times each and never successfully extracted the token. There was no discovery of the elaborate, inefficient method.

Experiment 1: Discussion

When chimpanzees used a well-established but laborious solution to successfully gain rewards, most were not seen to further explore alternatives, or to capitalise on social information available about a more efficient approach. The central finding from Experiment 1 was thus of a remarkable degree of conservatism, expressed in perseverance with a well-rehearsed routine despite witnessing a more efficient alternative modelled by another chimpanzee. Such conservatism has been documented in a series of other recent chimpanzee studies[13,16,18–21]. By contrast, in the 'naïve' group, the efficient method was discovered, if by only a single persistent individual, and was later adopted by another chimpanzee. The results thus tentatively suggest that having a prior solution may in itself hinder adoption of a superior alternative[16,18]. Such conservatism may have some adaptive value insofar as switching to an alternative may be costly, either through cognitive demands inherent to learning or potential loss

Individual	Sex	Age	Group	Wild/ captive	Rearing
My	F	49.26	Model	Wild	Unknown
Ma	F	48.26	Social info	Wild	Unknown
Cea	F	23.10	Social info	Captive	Mother
Ze	F	11.95	Social info	Captive	Mother
Ta	F	21.36	Social info	Captive	Mother
Co	F	30.24	Model	Captive	Mother
Se	F	15.40	Social info	Captive	Mother
Hh	F	23.93	Social info	Captive	Mother
Cr	M	18.78	Social info	Captive	Mother
An	M	22.86	Social info	Captive	Mother
Mi	F	24.69	Model	Captive	Mother
Sa	F	24.71	Social info	Captive	Mother
Je	F	24.96	Social info	Captive	Mother
Si	M	24.74	Social info	Captive	Mother
Kt	F	25.78	Non-seed	Captive	Nursery
Na	F	23.88	Non-seed	Captive	Nursery
Ae	F	39.39	Non-seed	Wild	Unknown
Ai	F	19.21	Non-seed	Captive	Nursery
Gs	M	22.41	Non-seed	Captive	Nursery
Chu	F	33.57	Non-seed	Captive	Mother
Sha	F	23.75	Non-seed	Captive	Mother
Ka	F	23.56	Non-seed	Captive	Mother
Jy	M	42.52	Naïve	Wild	Unknown
Ua	F	50.53	Naïve	Wild	Unknown
Cy	M	24.41	Naïve	Captive	Mother
Zy	M	43.52	Naïve	Wild	Unknown
Ha	F	48.53	Naïve	Wild	Unknown

Table 1. Demographics of participants meeting criterion for inclusion. From left to right: Individual: Initials of participant (individuals are organised by their groups with participants listed under their respective models); Sex: F = female, M = male; Age: Age in years at time of testing; Group: Social info = social information group; Non-seed = non-seeded; Naïve = Naïve group; Captive/wild: Captive = born in captivity, Wild = born in the wild; Rearing: Mother = raised by mother, Nursery = raised by human caretakers.

of reward through lack of expertise in this method[41,42]. In fact, chimpanzees, who at the start of the testing period were already well practiced at the inefficient method, effectively halved the time taken to successfully extract the token across the testing period. This indicates growing expertise and skill proficiency in their behaviour, and supports previous findings that skill mastery may hinder behavioural change[16,18].

To further investigate the limits of behavioural conservatism, in Experiment 2 the disparity in efficiency of behaviours was increased such that the inefficient method became not only an unreliable means of foraging but even when successfully employed, the latency to extraction from point A was typically far higher than for B. In addition, the alternative behaviour needed for extraction at point B was reduced to a single element and did not require use of parts of the inefficient method, so subjects had only to relinquish an established solution and adopt a novel one-stepped alternative with no ratcheting on prior behaviours.

Experiment 2: Relinquishing a highly inefficient solution

The movement of the token along the length of the apparatus to extraction point A was impeded by placing the token in an indentation in the floor, directly behind extraction point B (Fig. 1), so movement of the token towards A was more awkward to initiate. However, the token could now be extracted from point B solely by just pulling the door open. Raising lids and using finger holes was unnecessary. Accordingly, this experimental manipulation made the inefficient method more so, and the efficient method yet easier, enhancing the contrast between them (Supplementary Table S2).

The 19 subjects who had met criterion for inclusion in the 'social information' and 'non-seeded' groups were all given a further ten hours of opportunity for solution and open diffusion with the inefficient method partially blocked in this way. Following Yamamoto *et al.*[26], if individuals in the 'social information' groups failed to switch, they were provided with salient human demonstrations of the efficient method by SJD after this second period of open diffusion, because our question is not about chimpanzees offering such models, but rather how chimpanzees respond to such models when available. The 'naïve' group was not included in Experiment 2 as not only were they already exclusively using the efficient method of extraction, but their initial inclusion was designed primarily to investigate how solution naïve chimpanzees would approach this problem.

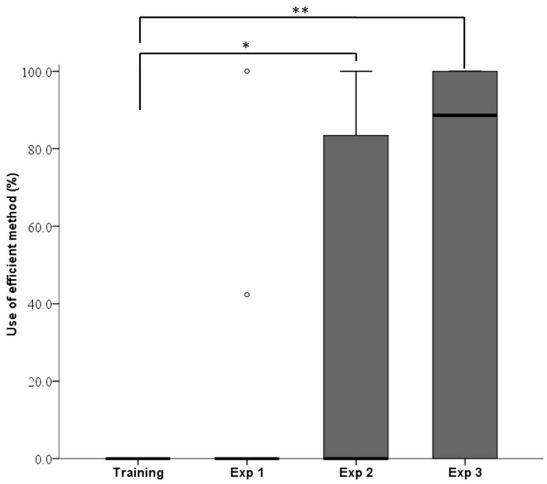


Figure 2. Percentage use of efficient method in Training and Experiments 1, 2 and 3 for individuals in the 'social information' groups. The line represents the median, the bottom and top of each box indicate the 25th and 75th percentile respectively, the whiskers show the minimum and the maximum values that are not considered outliers (i.e. values > 1.5 times the interquartile range from the 25th or 75th percentile), outliers are represented by circles with values over three times the 75th percentile value. *Indicates a P value of less than 0.05 and **less than 0.01.

Experiment 2: Results

Extractions within the test period. In the 'social information' groups, the chimpanzee models demonstrated a 100% success rate of token extraction via the efficient method; in contrast, use of the inefficient method had a median success rate of only 25% (range 0–93%) (Supplementary Tables S1 and S2: a failed attempt was one in which a participant manipulated the Serialbox but subsequently left the apparatus without successfully extracting the token). Success rate became significantly lower in Experiment 2 (E2) compared to Experiment 1 when using the inefficient method (One-tailed Wilcoxon Signed ranks test $Z = -2.84$, $n = 10$, $P = 0.001$, $median_{E1} = 100\%$, $median_{E2} = 25\%$, $r = -0.64$). If participants were successful in extracting the token via the inefficient method, latency to extraction was almost two and a half times longer than a successful extraction in Experiment 1 (E1 median = 33.6 seconds, range = 24.5–51.8; E2 median = 83 seconds, range 66.1–556; See Supplementary Table S2 for comparisons with models' efficiency).

In the 'non-seeded' groups, one individual now discovered and used the easier efficient method (Individual *Kt*), and was witnessed by two other individuals, *Na* and *Ae*. These two did not then acquire the method; however, they had observed *Kt* only three and two times respectively. No other individual was observed to use the efficient method in the 'non-seeded' groups, with success rate dropping for all other participants (median success rate of 14.3%, range 0–50%). Success rate was significantly lower in E2 than in E1 for those using the inefficient method in the 'non-seeded' groups (One-tailed Wilcoxon Signed ranks test $Z = -2.38$, $n = 7$, $P = 0.008$, $median_{E1} = 100\%$, $median_{E2} = 14.3\%$, $r = -0.64$). Success rate for those using the inefficient method did not differ between the 'social information' and 'non-seeded' groups (Mann Whitney $U = 28$, $n = 17$, $P = 0.494$).

Switching behaviours. To assess switching behaviours in the 'social information' groups, the percentage of efficient extractions [efficient extractions/(efficient extractions + inefficient extractions) × 100] observed throughout E2 for each participant was compared with the percentage of efficient extractions observed during E0, using a one-tailed Wilcoxon signed rank test. There was now a significant switch, with five individuals in the 'social information' groups switching from the inefficient method to using the more efficient method that continued to be demonstrated by the model [$Z = -2.023$, $n = 11$, $P = 0.031$, $median_{E0} = 0\%$ (mean = 0%), $median_{E2} = 0\%$ (mean = 36.1%), $r = -0.43$; Fig. 2].

Human demonstrations. After additional human demonstrations (median demonstrations given = 12, range = 10–17), four additional participants from the remaining six switched to using the efficient method in the 'social information' groups.

Use of efficient method in 'social information' and 'non-seeded' groups. To determine the role of social information in behavioural upgrading, a one-tailed Fisher's exact test (applied due to expected values less than 5) compared the frequency of chimpanzees using the alternative method between those in 'non-seeded' groups and the 'social information' groups. A significant association was found between exposure to sustained social information and whether or not individuals switched to using the efficient alternative ($P = 0.005$) (Fig. 3). Based on the odds ratio, the odds of switching were 31.5 times higher for those in the 'social information' groups than those in the 'non-seeded' groups. As noted above, the two individuals who observed *Kt* in the 'non-seeded' group performing the efficient method did not acquire it, but they observed only three and two times respectively, whereas those in the 'social-information' groups had a median of 31 observations before acquisition (range 15–169; Supplementary Table S3).

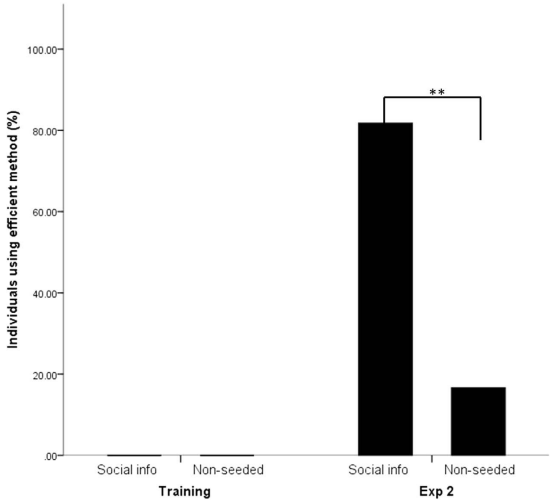


Figure 3. Percentage of individuals within the 'social information' groups and 'non-seeded' groups who used the efficient method across Training and Experiment 2. **Indicates a P value of less than 0.01.

Experiment 2: Discussion

In all, nine of the 11 chimpanzees in the 'social information' groups were eventually able to flexibly change their behaviours by relinquishing their mastered technique and switching to a novel one. We infer that this was due to the greater contrast between participants' inefficient use of extraction at point A and the more efficient use of extraction at point B displayed by the model, a contrast that involved differences in both latency to extraction and proportion of successful extractions.

An alternative possibility, that the changes occurred because of the more extended time frame of adding E2 to E1, affording more observations of the model, can be rejected for several reasons. First, E1 involved a long period in which any switching at all was rare, and moreover, participants not switching in E1 persevered with their inefficient technique despite both multiple observations of the model (median 18 observations, range 11–46) and multiple token extractions using their inefficient method (median 18 attempts, range 4–119 for those that switched in Experiment 2). In addition, among chimpanzees who did switch at some point, the number of observations of the efficient method did not predict the number of manipulations they would take before switching (final two columns in Supplementary Table S3). Given these considerations and that (i) only two participants were seen to open the door at point B in E1, and critically, (ii) no other individual was observed to make any persistent attempts to open the door until their behaviours became highly inefficient in E2, we conclude that the switch in behavioural strategy in E2 can be ascribed to the change in the relative efficiency of the options that were experimentally engineered between E1 and E2.

Five of the switching chimpanzees showed relatively low levels of behavioural conservatism, with two having previously upgraded their behaviours in E1, the other three adopting the alternative once their own approach became highly inefficient in E2. This was clearly facilitated by social information, as demonstrated by a lack of switching (bar one individual) in the 'non-seeded' groups. The social learning involved may have relied on only relatively simple processes such as stimulus enhancement (of token extraction at point B), or more complex ones, like emulation or imitation, and our study was not designed to discriminate among these. In any case, stimulus enhancement or any other social learning was insufficient for change despite extensive exposure in Experiment 1; it had effects only when the contrast in efficiency became more extreme.

Other chimpanzees still displayed a high degree of behavioural conservatism, in line with previous research[13,16,18–21], showing a difficulty in inhibiting use of a highly inefficient established behaviour, with varying levels of perseveration. This was most evident in the 'social information' groups, where despite many observations of a far more efficient alternative, six individuals continued in their old behaviour for some time, with four only switching behaviours following salient social information engineered though human demonstrations, and the two remaining individuals never relinquishing their inefficient solutions.

There was also very little exploratory behaviour in the 'non-seeded' groups, with only one individual discovering the efficient method. Despite witnessing the efficient solution, two individuals within the 'non-seeded' groups never attempted this alternative method. This was most likely due to their more limited and inconsistent exposure to demonstrations of this method, and highlights again the conservative nature of chimpanzee behaviour. Although there was no direct relationship between the number of observations of the model and number of manipulations taken before switching, no individual within the 'social-information' groups was seen to switch after as few demonstrations as experienced by these 'non-seeded' individuals, indicating the potential need for relatively sustained social information across repeated attempts to solve the Serialbox. This mirrors findings in humans whereby trial and error learning interacts with repeated exposure to socially available alternatives to produce behavioural change[43].

Whilst these results show some degree of behavioural flexibility, it remained to be seen whether chimpanzees could express such flexibility in a cumulative fashion; that is, could chimpanzees "add an existing technique used

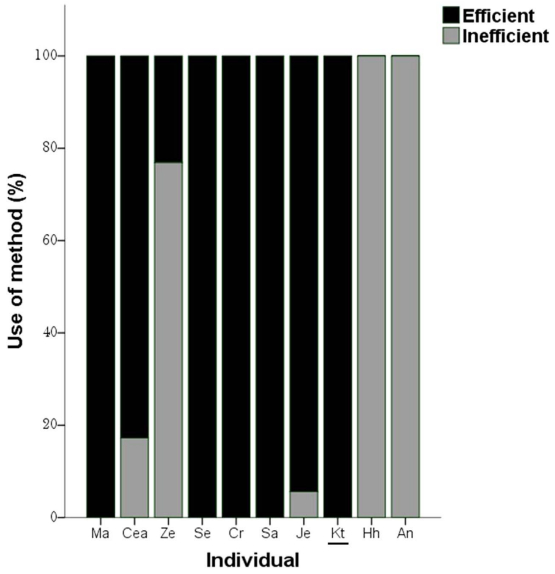


Figure 4. Percentage use of the inefficient and efficient solution of token extraction in Experiment 3 for each individual with prior experience of extraction via point B during Experiment 2. The 'non-seeded' individual *Kt* is underlined, with all other individuals being 'social-information' participants.

in a different context, or an entirely novel technique, to an existing technique, and integrate them functionally" (p. 181[44]): could they now integrate the efficient method they had acquired (door pull and extraction at point B) with behavioural elements common to the inefficient method (lid lifting and hole poking) to cumulatively produce the efficient solution demanded by the scenario used in Experiment 1? In Experiment 1 only two chimpanzees were observed to do this, with the majority instead sticking to their known behaviours despite potential gains in extraction efficiency. Now however, seven additional chimpanzees within the 'social information' groups and one from the 'non-seeded' groups had mastered use of an alternative, independent solution (door pull and extraction at point B), which could potentially be combined with other known behaviours (elements of the inefficient solution) to produce a compound technique that they were previously not seen to use when some of these elements were novel.

Experiment 3: Modifying, inhibiting and building on existing behaviours

To investigate chimpanzees' potential for such accumulation, the token was repositioned in the same location as in Experiment 1 (i.e. it was removed from the indent in the floor so its movement was no longer impeded), and could now be successfully extracted at either point A using the methods of E0, or from point B (Fig. 1). To extract from point B, individuals had to employ initial elements from their learned, inefficient technique (lid lifting and hole poking) but inhibit the remainder of the sequence resulting in extraction at point A and instead combine lid lifting and poking with the element unique to efficient extraction (the door pull at point B). Alternatively, individuals could now revert back to using their earlier well-practiced inefficient technique, with this method reliably yielding the token, but much more slowly.

Experiment 3: Results

Extractions within the test period. One individual in the 'social information' groups and three individuals in the 'non-seeded' groups chose not to participate during the test period ('E3'– Supplementary Table S1).

Switching behaviours. In the 'social information' groups, there was a significant change of behaviour from use of the earlier, trained inefficient method, with seven individuals now using the more efficient compound solution needed (One-tailed Wilcoxon signed rank test comparing percentage use of efficient behaviours: $Z = -2.410$, $n = 10$, $P = 0.008$, $median_{E0} = 0\%$, $median_{E3} = 88.2\%$, $r = -0.54$; Fig. 2). In the 'non-seeded' groups, one individual, *Kt,* also built on her prior solution to use the more efficient method. No additional individuals in the 'non-seeded' group used the efficient method of extraction, with four exclusively sticking with the inefficient solution.

At the individual level, of those with personal experience of the efficient method ($n = 9$ 'social information' participants and $n = 1$ 'non-seeded' participant), seven showed a significant change of behaviour from their initial inefficient method to using the efficient compound solution (one-tailed Fisher exact tests with Bonferroni corrected P value = 0.005), whilst three reverted back to preferentially using the inefficient method ($P > 0.005$). In sum, five exclusively used the efficient method, three flexibly switched between using both methods, and two exclusively returned to the inefficient method (Fig. 4 and Table 2).

Individual	Exp 1	Exp 2		Exp 3
	Old solution somewhat inefficient	Old solution highly inefficient	Human Demos	Old solution somewhat inefficient
Sa	Build	Switch	N/A	Build
Se	Build/revert	Switch	N/A	Build
Ma	Stay	Switch	N/A	Build
Cea	Stay	Switch	N/A	Build
Ze	Stay	Switch	N/A	Build
Kt	Stay	Switch	N/A	Build
Cr	Stay	Stay	Switch	Build
Je	Stay	Stay	Switch	Build
Hh	Stay	Stay	Switch	Revert
An	Stay	Stay	Switch	Revert
Ta	Stay	Stay	N/A	Stay
Si	Stay	Stay	Stay	N/A

Table 2. Summary of participant's behaviour in the 'social information' groups as well as the innovator (*Kt*) in the 'non-seeded' group. 'Build' denotes building on the inefficient solution. 'Stay' denotes maintaining use of the inefficient solution. 'Revert' denotes reverting back to the inefficient solution after having efficiently extracted through point B. 'Switch' denotes relinquishing the inefficient solution in favour of using the door and extraction at point B. 'N/A' represents no participation in this phase.

Experiment 3: Discussion

Seven chimpanzees in the 'social information' groups now displayed the efficient solution employed by the models. Only two of these individuals had previously been seen to use this efficient solution, when this required the addition of a novel element, in E1. The other five, along with the innovator *Kt* in the non-seeded' group, displayed a cumulatively built combination of elements they had learned in E0 and E2. From the results of E3 we conclude that accumulation involved the combination of behaviour routines already in the repertoire. One of these, opening the door at point B (even if it was the case that this was acquired only by affordance learning about the significance of this door, but also if it involved copying the action sequence involved), gave rise to behavioural routines that could be combined with parts of an earlier-acquired procedure, of opening lids and poking, learned via training in E0. Chimpanzees' successes in E3 additionally displayed an ability to flexibly inhibit the remainder of the trained routine for extraction at point A. Such capacities for cumulative combination, although modest compared to full cumulative culture, could, we submit, provide important foundations for cumulative culture if present in ancestral states.

General Discussion

Chimpanzees were trained to use a relatively laborious sequence of actions to extract a valuable food-token from a puzzle-box. This initial method was sufficiently complex to require socially-facilitated acquisition in most chimpanzees and we ensured it was then extensively practiced, to become routine, as in cultural behaviours in the wild. A different, more efficient alternative was then demonstrated by a high ranking female conspecific. This new solution involved partial use of behaviours in common with the established extraction technique as well as the addition of a novel element.

When chimpanzees could still successfully forage with their established method (in E1), only a small minority relinquished this and flexibly upgraded to the more efficient alternative witnessed. The predominant failure to switch to the more efficient technique is consistent with earlier reports of chimpanzee conservatism[13,16,18–21] and may offer a partial explanation for the relative stasis of chimpanzee culture. However, when their established behaviours were made considerably more inefficient in E2, most chimpanzees observing a knowledgeable individual were able to relinquish their inefficient behaviour and flexibly switch to using an alternative strategy. When in E3 they were again challenged by the task configuration of E1, the majority of these chimpanzees showed an ability to build on prior behaviours by combining already acquired elements of their learned use of the door for extraction at point B and parts of their earlier technique for extraction at point A. They had not achieved this earlier in E1, when success required the addition of a *novel* behaviour to the sequence. The cumulative combinations recorded in E3 thus stand in contrast to the findings of previous studies where chimpanzees appear behaviourally inflexible[13,16]. Our results suggest that in certain contexts at least, chimpanzees may combine *known* behaviours to match an efficient compound technique demonstrated by others.

Although chimpanzees show a considerable degree of behavioural conservatism, we suggest these results indicate that they also have an ability to combine independent behaviours to produce more efficient compound action sequences. Such an ability, while not yet truly cumulative, may be one of the foundational abilities (or candidate mechanisms) for human cumulative culture, through the ability to "add an existing technique used in a different context ….to an existing technique, and integrate them functionally" (p.181[44]). This shares similarities with human studies in which recombination of behavioural variants is employed to move solutions closer to an optimum[45–50]; that is, accumulation may commonly be brought about through novel recombination of existing behaviours, creating "innovations without invention, creativity or trial and error learning" (p.5[49]).

Whilst we offer evidence for a potential core prerequisite of cumulative culture, this is not evidence of cumulative culture itself, as the behaviours of interest were also produced spontaneously by one chimpanzee we studied, and they do not require the combination of multi-generational contributions by several innovators, which is inherent to full-blown cumulative culture[10]. Further, our study was not designed to dissect exactly how the chimpanzees were learning from the available social information, whereas advanced cultural accumulation is thought to depend on high fidelity transmission[51], as well as cognitively complex learning heuristics[15,52]. However, chimpanzees in our study were able to use multiple solutions as well as to build on and combine prior behaviours to efficiently solve an extractive foraging problem, indicating greater potential for cumulative change than found in many earlier studies and emphasized in recent reviews (e.g. ref. 53). The accumulation observed here lends support to the plausibility that some behaviour exhibited by wild chimpanzees is actually the result of a cumulative process, even if elementary compared to that observed in human culture[54–58].

Experiment 1: Methods

Subjects and housing. N = 43 individuals (18 males; average age: 29.1; range: 11.9–50.5 years; Table 1) were group housed at the National Center for Chimpanzee Care at the Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center in Bastrop, Texas, U.S.A. Group size ranged from 5–10 individuals. Chimpanzees were trained and tested in both their outside enclosures (ranging in size from corrals at 4,300 square feet to Primadomes™ measuring approximately 34 feet in diameter and 25 feet high) and indoor dens (ranging in size from 6 feet deep by 15 feet wide to approximately 8 feet and 8 inches deep by 9 feet wide). Individuals were given the opportunity to voluntarily participate and separate from their group for further training and testing purposes in their inside enclosures for a period of no longer than 30 minutes. Participants were not food or water deprived during training or testing.

Apparatus. A transparent, elongated, Plexiglas 'Serialbox', measuring 61 centimetres long, five centimetres high and five centimetres wide, was attached to a mobile cart and pushed to the mesh of enclosures. Along the length of the transparent Serialbox were four compartments (Fig. 1). Each compartment had a hinged lid on top which could be lifted open. Under each lid were four finger holes (2.5 cm in diameter) that permitted an object initially placed inside the box at the left-most end from the chimpanzees' perspective to be pushed the length of the apparatus. This object could then be extracted through an opening at the other end of the Serialbox ('Extraction point A' in Fig. 1). A small door spanning two thirds of the first compartment was fitted on the chimpanzee side of the apparatus and could be pulled open using a handle protruding outside the box to give alternative and quicker access to the left-most compartment ('Extraction point B' in Fig. 1), where the token was initially positioned.

Procedure. *Training phase (5 groups, 38 chimpanzees).* Chimpanzees were initially trained to associate a small purple plastic token with a reward by trading this with experimenter SJD in exchange for one grape. The token was then placed inside the apparatus three quarters of the way along the first compartment (Fig. 1). The inefficient method of retrieving the token was demonstrated by SJD three times before participants interacted with the Serialbox. The inefficient method involved the lifting of each of the lids of the four compartments providing access to the finger holes. These holes were used to ferry the token along the compartments of the apparatus until it could be extracted from point A (Supplementary Video 1). Following these demonstrations, the box was pushed to the mesh allowing all individuals in each group access. Once the token was extracted from the apparatus, it was exchanged with SJD for one grape. During the training phase, the efficient method was not available because the pull door was locked shut, preventing extraction from point B. If an individual was not able to successfully retrieve the token after demonstrations, scaffolding of the solution was provided whereby the token was positioned adjacent to extraction point A until extraction from this point was mastered, with additional demonstrations given if necessary. The token was gradually placed further away until the chimpanzee was manoeuvring the token along the length of the apparatus by opening the lids and using the underlying finger holes. Participants were given the opportunity to engage with the Serialbox until all participating individuals had successfully retrieved the token a minimum of twenty times over no fewer than two training sessions. When an individual was successful in retrieving the token, the apparatus was pulled back from the mesh, reset and re-baited. If an individual showed interest in operating the apparatus but was unable to gain access due to monopolisation by more dominant individuals, they were offered the opportunity to voluntarily enter their indoor enclosures and participate by themselves until they had reached criterion for inclusion in the study.

Social information groups: Presence of social demonstrator (Three groups, N = 26). Model training phase. After all participating chimpanzees had reached criterion, a high ranking female chimpanzee voluntarily separated from her group and was trained on how to solve the Serialbox using a more efficient method. This involved pulling the door open, and, due to the positioning of the token a short distance from the extraction point (Fig. 1), lifting one lid and using the underlying finger holes to manoeuvre the token towards point B for efficient retrieval (Supplementary Video 2). Training sessions lasted around twenty minutes.

Social demonstration phase. The Serialbox was re-introduced to the entire group with the efficient method no longer locked. The token could now be retrieved via either extraction point A or B. The model was called by name and vocally encouraged to demonstrate the efficient method, which all models complied with. Following each extraction, the token was exchanged with SJD for one grape. After each participant had witnessed at least ten demonstrations of the more efficient method over no fewer than two separate testing sessions, the entire group was given the opportunity to interact with the Serialbox. A demonstration was taken to occur if an individual was within two metres of the model and the potential observer's head was orientated towards the apparatus. If

a participating individual did not come into proximity with the model during the social demonstration phase, they were given the opportunity to voluntarily separate with the model and observe her actions. After the model had successfully retrieved the token, the apparatus was pulled away from the demonstrator, reset and re-baited.

Testing phase (N = 11). The apparatus was presented over ten hours to all participating individuals with both the efficient and inefficient methods as viable strategies to extract the token. After each successful extraction, the apparatus was pulled away, reset and re-baited. To avoid cueing of responses, SJD occluded the apparatus and her hand movements with a sheet during interactions with the box. The apparatus was not made available to any non-participating chimpanzee (i.e. any individual who had not met criterion to be included in the study).

Non-seeded groups: No social demonstrator (Two groups, N = 12). Control groups experienced the Training phase and Testing phase as above, but no model seeded knowledge of the more efficient method.

Naïve group (1 group, N = 5). This control group was exposed to the apparatus with no prior knowledge of any solution over ten hours of open diffusion. Both the efficient and inefficient methods were viable extraction techniques.

Experiment 2: Methods

Methods followed those outlined in the Testing phase of Experiment 1 Methods with the exception that the token was now placed in an indent in the floor located directly behind (from the chimpanzee's perspective) extraction point B (Fig.1). This impeded movement of the token along the length of the apparatus. The 'naïve' group was not included in Experiment 2. Following Yamamoto *et al.*[26], if individuals within the 'social information' groups failed to switch, they were provided with salient demonstrations of the efficient method by SJD after this second period of open diffusion (one individual did not receive human demonstrations as she did not wish to separate from her group). To avoid unnecessary voluntary separation of participants from their group, so long as a participant was able to gain access to the Serialbox, human demonstrations were given in the presence of other group members. If instead the participant struggled to gain access, they were offered the opportunity to voluntarily separate and given additional demonstrations over a period lasting no more than 30 minutes. After the participant attempted the inefficient method, SJD pulled the apparatus back and demonstrated use of the door. If participants were still attempting to use the inefficient method, SJD provisioned the apparatus with the door already open, facilitating extraction via point B.

Experiment 3: Methods

The token was again placed inside the apparatus three quarters of the way along the first compartment (as in Experiment 1). The apparatus was presented over five hours to all participating chimpanzees (19 individuals across the 'social information' and 'non-seeded' control groups), with both the efficient and inefficient methods as viable strategies to extract the token, following the procedure outlined in the Testing phase of Experiment 1 Methods.

Analyses. Records of the social demonstration and testing phases were both narrated and visually recorded using a HC-920 Panasonic camcorder. Responses were coded *in situ* for all groups, with 'social information' groups' behaviour additionally coded through video analysis.

Ethics Statement. Ethical approval was granted for this study by the UTMDACC Institutional Animal Care and Use Committee (IACUC approval number 0894-RN01) and the University of St Andrews' Animal Welfare and Ethics Committee, and was carried out in accordance with approved guidelines.

References

1. Laland, K. N. & Hoppitt, W. Do animals have culture? *Evol. Anthr.* **12,** 150–159 (2003).
2. Tomasello, M., Kruger, A. C. & Ratner, H. H. Cultural learning. *Behav. Brain Sci.* **16,** 495–552 (1993).
3. Boyd, R. & Richerson, P. J. Why culture is common, but cultural evolution is rare. *Proc. Br. Acad.* **88,** 77–93 (1996).
4. Heyes, C. M. Social learning in animals: categories and mechanisms. *Biol. Rev.* **69,** 207–231 (1994).
5. Heyes, C. M. & Galef, B. G. *Social Learning in Animals: The Roots of Culture* (Elsevier, Amsterdam, 1996).
6. Hoppitt, W. & Laland, K. *Social Learning: An Introduction to Mechanisms, Methods, and Models* (Princeton University Press, Princeton, 2013).
7. Galef, B. G. Jr. & Whiten, A. The comparative psychology of social learning In *APA Handbook of Comparative Psychology* (APA, Washington, in press).
8. Reader, S. M. & Biro, D. Experimental identification of social learning in wild animals. *Learn. Behav.* **38,** 265–283 (2010).
9. Zentall, T. R. & Galef, B. G. Jr. *Social Learning: Psychological and Biological Perspectives* (Lawrence Erlbaum Associates, Hillsdale, 1988).
10. Tennie, C., Call, J. & Tomasello, M. Ratcheting up the ratchet: on the evolution of cumulative culture. *Phil. Trans. R. Soc. B* **364,** 2405–2415 (2009).
11. Whiten, A. *et al.* Cultures in chimpanzees. *Nature* **399,** 682–685 (1999).
12. Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E. & Kendal, R. L. Human cumulative culture: a comparative perspective. *Biol. Rev.* **89,** 284–301 (2014).
13. Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B. & Laland, K. N. Identification of the social and cognitive processes underlying human cumulative culture. *Science* **335,** 1114–1148 (2012).
14. Call, J., Carpenter, M. & Tomasello, M. Copying results and copying actions in the process of social learning: chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Anim. Cogn.* **8,** 151–163 (2005).
15. Laland, K. N. Social learning strategies. *Learn. Behav.* **32,** 4–14 (2004).
16. Marshall-Pescini, S. & Whiten, A. Chimpanzees (*Pan troglodytes*) and the question of cumulative culture: an experimental approach. *Anim. Cogn.* **11,** 449–456 (2008).

17. Lehner, S. R., Burkart, J. M. & van Schaik, C. P. Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques? *J. Comp. Psychol.* **125,** 446–455 (2011).
18. Hrubesch, C., Preuschoft, S. & van Schaik, C. Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (*Pan troglodytes*). *Anim. Cogn.* **12,** 209–216 (2009).
19. Bonnie, K. E. *et al.* Flexibility and persistence of chimpanzee (*Pan troglodytes*) foraging behavior in a captive environment. *Am. J. Primatol.* **74,** 661–668 (2012).
20. Hopper, L. M., Schapiro, S. J., Lambeth, S. P. & Brosnan, S. F. Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Anim. Behav.* **81,** 1195–1202 (2011).
21. Price, E. E., Lambeth, S. P., Schapiro, S. J. & Whiten, A. A potent effect of observational learning on chimpanzee tool construction. *Proc. R. Soc. B* **276,** 3377–3383 (2009).
22. Haun, D. B. M., van Leeuwen, E. J. C. & Edelson, M. G. Majority influence in children and other animals. *Devel. Cogn. Neurosc.* **3,** 61–71 (2013).
23. Horner, V. & Whiten, A. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Anim. Cogn.* **8,** 164–181 (2013).
24. Flynn, E. Investigating children as cultural magnets: do young children transmit redundant information along diffusion chains? *Phil. Trans. R. Soc. B* **363,** 3541–3551 (2008).
25. Tennie, C., Walter, V., Gampe, A., Carpenter, M. & Tomasello, M. Limitations to the cultural ratchet effect in young children. *J. Exp. Child. Psychol.* **126,** 152–160 (2014).
26. Yamamoto, S., Humle, T. & Tanaka, M. Basis for cumulative cultural evolution in chimpanzees: social learning of a more efficient tool-use technique. *PloS One* **8,** e55768 (2013).
27. Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W. & Gruber, T. Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biol.* **12,** e1001960 (2014).
28. Luncz, L. V., Wittig, R. M. & Boesch, C. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). *Phil. Trans. R. Soc. B* **370,** 20140348 (2015).
29. Sirianni, G., Mundry, R. & Boesch, C. When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees. *Anim. Behav.* **100,** 152–165 (2015).
30. Stokes, E. & Byrne, R. Cognitive capacities for behavioural flexibility in wild chimpanzees (*Pan troglodytes*): the effect of snare injury on complex manual food processing. *Anim. Cogn.* **4,** 11–28 (2001).
31. Wilfried, E. E. G. & Yamagiwa, J. Use of tool sets by chimpanzees for multiple purposes in Moukalaba-Doudou National Park, Gabon. *Primates* **55,** 467–472 (2014).
32. Hockings, K. J. *et al.* Apes in the Anthropocene: flexibility and survival. *Trends Ecol. Evol.* **30,** 215–222 (2015).
33. Hopper, L. M., Kurtycz, L. M., Ross, S. R. & Bonnie, K. E. Captive chimpanzee foraging in a social setting: a test of problem solving, flexibility, and spatial discounting. *PeerJ* **3,** e833 (2015).
34. van Leeuwen, E. J. C., Cronin, K. A., Schütte, S., Call, J. & Haun, D. B. M. Chimpanzees (*Pan troglodytes*) flexibly adjust their behaviour in order to maximize payoffs, not to conform to majorities. *PloS One* **8,** e80945 (2013).
35. Grandjean, J. & Collette, F. Influence of response prepotency strength, general working memory resources, and specific working memory load on the ability to inhibit predominant responses: A comparison of young and elderly participants. *Brain. Cogn.* **77,** 237–247 (2011).
36. Roberts, R. J., Hager, L. D. & Heron, C. Prefrontal Cognitive Processes : Working Memory and Inhibition in the Antisaccade Task. *J. Exp. Psychol.* **123,** 374–393 (1994).
37. Roberts, R. J. & Pennington, B. F. An interactive framework for examining prefrontal cognitive processes. *Dev. Neuropsychol.* **12,** 105–126 (1996).
38. Manrique, H. M., Völter, C. J. & Call, J. Repeated innovation in great apes. *Anim. Behav.* **85,** 195–202 (2013).
39. Whiten, A. & Mesoudi, A. Review. Establishing an experimental science of culture: animal social diffusion experiments. *Phil. Trans. R. Soc. B* **363,** 3477–3488 (2008).
40. Whiten, A., McGuigan, N., Marshall-Pescini, S. & Hopper, L. M. Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Phil. Trans. R. Soc. B* **364,** 2417–2428 (2009).
41. Reader, S. M. & Laland, K. N. *Animal Innovation* (Oxford University Press, Oxford, 2003).
42. Cohen, J. D., McClure, S. M. & Yu, A. J. Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. *Phil. Trans. R. Soc. B* **362,** 933–942 (2007).
43. Wiley, J. Expertise as mental set : The effects of domain knowledge in creative problem solving. *Mem. Cognition*, **26,** 716–730 (1998).
44. Pradhan, G. R., Tennie, C. & van Schaik, C. P. Social organization and the evolution of cumulative technology in apes and hominins. *J. Hum. Evol.* **63,** 180–190 (2012).
45. Boyd, R., Richerson, P. J. & Henrich, J. The cultural niche: Why social learning is essential for human adaptation. *PNAS* **108,** 10918–10925 (2011).
46. Derex, M., Feron, R., Godelle, B. & Raymond, M. Social learning and the replication process : an experimental investigation. *Proc. R. Soc. B* **282,** 20150719 (2015).
47. Enquist, M., Ghirlanda, S. & Eriksson, K. Modelling the evolution and diversity of cumulative culture. *Phil. Trans. R. Soc. B* **366,** 412–423 (2011).
48. Kempe, M. & Mesoudi, A. An experimental demonstration of the effect of group size on cultural accumulation. *Evol. Hum. Behav.* **35,** 285–290 (2014).
49. Muthukrishna, M., Shulman, B. W., Vasilescu, V. & Henrich, J. Sociality influences cultural complexity. *Proc. R. Soc. B* **281,** 20132511 (2014).
50. Youn, H., Strumsky, D., Bettencourt, L. M. A. & Lobo, J. Invention as a combinatorial process: evidence from US patents. *J. R. Soc. Interface* **12,** 20150272 (2016).
51. Lewis, H. M. & Laland, K. N. Transmission fidelity is the key to the build-up of cumulative culture. *Phil. Trans. R. Soc. B* **367,** 2171–2180 (2012).
52. Tomasello, M., Carpenter, M. & Hobson, R. P. The emergence of social cognition in three young chimpanzees. *Monog. Soc. Res. Child Dev.* **70,** i+vii+1–152 (2005).
53. Henrich, J. *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter* (Princeton University Press, New Jersey, 2015).
54. Boesch, C. Is culture a golden barrier between human and chimpanzee? *Evol. Anthr.* **12,** 82–91 (2003).
55. Boesch, C., Head, J. & Robbins, M. M. Complex tool sets for honey extraction among chimpanzees in Loango National Park, Gabon. *J. Hum. Evo.* **56,** 560–569 (2009).
56. Sanz, C., Call, J. & Morgan, D. Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). *Biol. Lett.* **5,** 293–296 (2009).
57. Sanz, C. M., Schöning, C. & Morgan, D. B. Chimpanzees prey on army ants with specialized tool set. *Am. J. Primatol.* **72,** 17–24 (2010).
58. Humle, T., Snowdon, C. T. & Matsuzawa, T. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Anim. Cogn.* **12,** S37–S48 (2009).

Acknowledgements

We thank the care staff for their invaluable expertise and assistance throughout the project and for the high standard of care and enrichment given to the chimpanzees, making this research possible. We are very grateful to Keith Haynes and Robert Mackenzie for the construction of the Serialbox and for designing Fig. 1, and William Nyberg for his technical and logistical support throughout this study. We thank Lisa Reamer for her advice and suggestion to use a token reward, Stuart Watson for providing interrater reliability and Richard Byrne for his constructive feedback on an earlier version of this manuscript. This research was funded by the John Templeton Foundation (Grant ID: 40128, to K. Laland and A. Whiten). Support for the chimpanzee colony came from NIH U42 OD-011197.

Author Contributions

S.J.D., A.W. and G.L.V. conceived the experiments. S.J.D. conducted the experiments and analysed the results. S.J.D. and A.W. wrote the manuscript. S.J.S and S.P.L provided essential logistical support. All authors reviewed the manuscript.

Additional Information

Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Davis, S. J. *et al.* Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Sci. Rep.* **6**, 35953; doi: 10.1038/srep35953 (2016).

11 November 2013

Project Title:	Innovation and Cumulative Culture in Chimpanzees
Researchers' Names:	Dr Gillian Vale, Sarah Davis and Professor Andrew Whiten
Supervisor:	Professor Andrew Whiten

Thank you for submitting your application which was considered at the Psychology & Neuroscience School Ethics Committee meeting on the 23rd October 2013. The following documents were reviewed:

1. Animal Ethics Form 01/11/2013

The School of Psychology & Neuroscience Ethics Committee approves this study from an ethical point of view.

Approval is given for three years. Projects, which have not commenced within two years of original approval, must be re-submitted to the School Ethics Committee.

You must inform the School Ethics Committee when the research has been completed. If you are unable to complete your research within the 3 three year validation period, you will be required to write to the School Ethics Committee to request an extension or you will need to re-apply.

Any serious adverse events or significant change which occurs in connection with this study and/or which may alter its ethical consideration, must be reported immediately to the School Ethics Committee, and an application for ethical amendment Form submitted where appropriate.

Approval is given on the understanding that the ASAB Guidelines for the Treatment of Animals in Behavioural Research and Teaching (published in Animal Behaviour, 2003, 65, 249-255, http://www.sciencedirect.com/) are adhered to.

Yours sincerely

Convenor of the School Ethics Committee

Ccs Professor Andrew Whiten (Supervisor)
School Ethics Committee
Dr Tamara Lawson (Home Office Liaison Officer)